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Inner Bay of Fundy Atlantic salmon (*Salmo salar*) critical habitat case study

Étude de cas de l'habitat essentiel du saumon atlantique (*Salmo salar*) de l'intérieur de la baie de Fundy

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ABSTRACT

Atlantic salmon in the inner Bay of Fundy (iBoF) were common only 30 years ago, but they have declined to such critically low levels that they are now at risk of being extirpated. The Species at Risk Act requires that recovery plans for endangered, threatened and extirpated species include the identification and protection of critical habitat. The purpose of this document is to evaluate the relationships between habitat quality and quantity and the survival and recovery of iBoF Atlantic salmon in order to determine whether habitat protection will aid in this population's recovery. This evaluation is based on: 1) present status of iBof salmon, 2) an assessment of the amount of freshwater habitat available for iBoF salmon, 3) a review of recovery targets for these populations, 4) a statistical analysis of the life history of an iBoF salmon population to assess which life history parameters changed, and when, 5) equilibrium analyses of population size and viability and 6) a population viability analysis (PVA) to determine whether habitat protection would aid in population recovery.

Despite having over 9,000,000 m^2 of habitat available in over 22 rivers, iBoF salmon are at very low levels and extirpations have occurred in several rivers. Juvenile salmon are present in rivers with Live Gene Bank (LGB) support, but densities are extremely low in rivers without support. Two possible recovery targets are considered: the conservation limits used for fisheries management and the population size to maintain genetic variability (N_e). The former places recovery targets in the range of 280 small and 420 large salmon for the Big Salmon River and 772 small and 289 large salmon for the Stewiacke River, and the latter in the range of 568 to 1,923 salmon per river.

Analysis of the dynamics of salmon in the Big Salmon River indicate that the annual mortality of immature salmon at sea increased from 0.83 (pre-1990 time period) to 0.97 (post-1990 time period) and that annual mortality of post-spawning adults has increased from 0.49 to 0.64 during the same time. Under present conditions, the equilibrium population is zero and the expectation is that, in the absence of human intervention, the population will go extinct on the time scale of 10 to 15 years. Intervention in the form of captive rearing through the LGB program has at least slowed the decline in some rivers. Both the equilibrium analyses and PVA indicate that population viability cannot be enhanced through changes in freshwater habitat quantity, although persistence of very small populations may be somewhat enhanced through increases in freshwater habitat quality. A change in marine survival is required to reach recovery targets. If marine survival increases, recovery times are sensitive to the quantity and quality of freshwater habitat. These results indicate that a freshwater habitat protection will not reverse current declines but could be important for population recovery if marine survival increases. At present, insufficient data exists to evaluate the efficacy of marine habitat protection for recovering iBoF salmon.

RÉSUMÉ

Il n'y a que trente ans, le saumon atlantique de l'intérieur de la baie de Fundy était abondant, mais ses effectifs ont connu un tel déclin qu'il est maintenant en danger de disparaître du pays. La *Loi sur les espèces en péril* exige que les plans de rétablissement d'espèces disparues du pays, en voie de disparition ou menacées incluent l'identification et la protection de l'habitat essentiel. L'objectif du présent document est d'évaluer les relations entre, d'une part, la qualité et la quantité de parcelles d'habitat et, d'autre part, la survie et le rétablissement du saumon atlantique de l'intérieur de la baie de Fundy en vue d'établir si la protection de l'habitat l'aidera à se rétablir. La présente évaluation est fondée sur : 1) l'état actuel des populations de saumon atlantique de l'intérieur de la baie de Fundy, 2) une évaluation de la quantité de parcelles d'habitat d'eau douce à la disponibilité de ces populations, 3) un examen des cibles de rétablissement pour ces populations, 4) une analyse statistique du cycle vital d'une de ces populations visant à établir quels paramètres ont changé et quand cela s'est produit, 5) des analyses à l'équilibre de la taille et de la viabilité des populations et 6) une analyse de la viabilité des populations (AVP) visant à établir si la protection de l'habitat les aidera à se rétablir.

Bien qu'elles disposent de plus de 9 000 000 m^2 d'habitat dans quelque 22 cours d'eau, les populations de saumon atlantique de l'intérieur de la baie de Fundy ont accusé une chute spectaculaire; maintenant décimées, elles ont aussi disparu de plusieurs cours d'eau. Des juvéniles sont retrouvés dans les cours d'eau bénéficiant d'un apport de la banque de gènes vivants, mais leurs densités sont extrêmement faibles dans ceux qui n'en bénéficient pas. Deux cibles de rétablissement possibles sont considérées : la limite propre à assurer la conservation utilisée aux fins de gestion des pêches et la taille des populations propre à assurer la variabilité génétique (N_e). Selon la première, les cibles de rétablissement se situeraient à environ 280 petits et 420 gros saumons pour la rivière Big Salmon et 772 petits et 289 gros saumons pour la rivière Stewiacke, et la seconde, à environ 568 à 1 923 saumons par rivière.

L'analyse de la dynamique de la population de saumon de la rivière Big Salmon indique que le taux de mortalité annuel des individus immatures en mer a augmenté, de 0,83 avant 1990 à 0,97 après 1990, et que le taux de mortalité annuel des charognards a augmenté aussi, de 0,49 à 0,64. Dans les conditions actuelles, la population à l'équilibre est nulle et l'attente est que, en l'absence d'une intervention humaine, cette population disparaîtra d'ici 10 à 15 ans. L'intervention prenant la forme de l'élevage en captivité dans le cadre du programme de la banque de gènes vivants a au moins ralenti le déclin des populations dans certaines rivières. Les analyses à l'équilibre et l'AVP indiquent que la viabilité des populations ne peut être accrue par le biais de changements dans le nombre de parcelles d'habitat en eau douce, quoique la persistance de populations très petites peut être un tant soit peu bonifiée par le biais d'une amélioration de la qualité de l'habitat en eau douce. Il faut que le taux de survie en mer augmente pour que les cibles de rétablissement soient atteintes. Si cela est le cas, le temps qu'il faudra pour que les populations se rétablissent dépend de la quantité et de la qualité des parcelles d'habitat en eau douce. Les résultats obtenus révèlent que la protection de l'habitat en eau douce ne renversera pas les déclins en cours, bien qu'elle pourrait jouer un rôle important au titre du rétablissement des populations si le taux de survie en mer augmente. L'insuffisance des données disponibles à l'heure actuelle ne permet pas d'évaluer l'efficacité de la protection de l'habitat marin au titre du rétablissement du saumon de l'intérieur de la baie de Fundy.

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1.0 Introduction

Canada recently made a formal commitment to the preservation and restoration of Canada's flora and fauna by the passing of the Species at Risk Act (SARA). The act makes Canadians responsible for identifying and, if possible, alleviating factors that lead to a species' extirpation or extinction, thereby reducing the overall loss of biodiversity. All species require space and resources to complete their life cycle. These requirements are often lumped into what is called 'habitat'. Therefore, by definition, habitat is necessary to ensure population persistence. The threat to species persistence created by habitat loss and degradation is recognized under SARA. Under the act, once a species is listed, recovery planning is mandatory and must include identification and protection of critical habitat for endangered, threatened and extirpated species. SARA defines 'critical habitat' as "habitat that is necessary for the survival or recovery of a listed wildlife species and that is identified as the species' critical habitat in the recovery strategy or in an action plan for the species".

In December, 2002, the Department of Fisheries and Oceans convened a national science workshop on critical habitat to identify quantitative, science-based methods for measuring critical habitat for aquatic species-at-risk, including methods of demonstrating cause and effect linkages between species habitat and species survival prior to critical habitat designation (Randall et al. 2003). This workshop led to a set of case studies to evaluate how such linkages could be developed, including this evaluation of whether a critical habitat designation would affect the population viability of inner Bay of Fundy (iBoF) Atlantic salmon (*Salmo salar*). Additionally, at the workshop, the roles of the knowledge level about the species' life history, distribution and habitat requirements were also identified as a factor that could influence a critical habitat designation for the species. IBoF salmon were included as one of the case studies because its life history is well studied, the species has a broad distribution, is migratory, and is "data-rich" in comparison with many listed species (i.e., it is relatively well studied).

The purpose of this document is to assess whether a critical habitat designation could aid in the survival and recovery of iBoF Atlantic salmon. This assessment follows the draft guidelines for the identification of critical habitat under SARA (Prior 2003), and one purpose of this analysis is to provide a partial evaluation of these guidelines as they pertain to aquatic species. Included herein are:

- A review of information pertaining to the life history of iBoF Atlantic salmon including shortcomings and uncertainties,
- Information pertaining to the historic and present distribution and abundance of iBoF salmon,
- Documentation of the habitat requirements for all life stages, and
- Deterministic and stochastic population viability analyses using habitat quality and quantity as the management control variable.

Because Atlantic salmon are diadromous, we attempt to address habitat requirements in both freshwater and marine environments. Additionally, a Live Gene Bank (LGB) program designed to limit the risk of extirpation of iBoF salmon was initiated in 1998. The purpose of this program is to maintain the potential for iBoF salmon recovery by

preserving the genetic base thought to be representative of the population. The program consists of two components: the "captive" and "in-river" live gene banks. Fish of various ages, from eggs to adults, are being held in captivity to help prevent the loss of these stocks. Salmon of various ages are then released into the rivers to provide exposure to the natural environment to allow natural selection to occur. A portion of these fish are then captured and brought back into the captive component of the program and mated according to a prescribed strategy. Habitat is required for the "in-river" component of the LGB, although whether a requirement exists for specific habitat in specific locations is not known. The conclusions drawn from these analyses, including limitations and shortcomings, and directions for future research are also discussed.

2.0 Inner Bay of Fundy Atlantic salmon

2.1 Background

IBoF Atlantic salmon are presently at critically low levels and were listed as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in May, 2001. This assemblage includes salmon native to rivers in the Bay of Fundy, northeast of the Saint John River, NB, and northeast of the Annapolis River, NS, exclusive of these rivers (Figure 2.1). Most populations in this assemblage are native to rivers in either the Minas Basin or Chignecto Bay. At least one other distinct Atlantic salmon assemblage is present within the Bay of Fundy. Outer Bay of Fundy populations tend to be larger and most females mature after two winters at sea, while males mature after one sea-winter. IBoF salmon show a high incidence of maturation after one sea-winter for both males and females (Amiro 2003a). IBoF salmon are considered distinct from these populations because iBoF salmon show similarities in characteristics such as smolt age, frequency of repeat spawning, age-at-maturation, size-at-age, and run timing of adults and smolts that collectively are not common elsewhere (Amiro 2003a). Commercial catches of iBoF salmon do not correlate with catches of other salmon populations (Huntsman 1931, Amiro 1990). Additionally, genetic analyses using microsatellite DNA (King et al. 2001, Jones 2001), and mitochondrial DNA (Verspoor et al. 2002) indicate that iBoF rivers contain salmon populations with a high degree of reproductive isolation from other populations.

2.2 Abundance and distribution: past and present

Based on reported recreational catch and electrofishing data, Atlantic salmon are known to have occupied at least 32 rivers around the inner Bay of Fundy (Amiro 2003a), although salmon may have also occupied other rivers in this area in the past. These data are summarized in Gibson et al. (2003a), and the past abundance is evidenced from the recreational catch (Table 2.1). Two rivers, the Big Salmon River, New Brunswick, and Stewiacke River, Nova Scotia, accounted for more than half of the recreational catch. IBoF salmon were also fished commercially within the inner Bay prior to 1985 (Amiro 2003a). Unfortunately, the commercial landings are difficult to interpret because the boundaries of the Fisheries Statistical Districts do not coincide with the present geographic boundaries for iBoF salmon, regulations and effort have changed through time, and fisheries located in marine and estuarine waters may intercept fish from other population assemblages. The landings for Albert and Westmorland counties, NB, ranged from a high of 29,892 kg in 1915 to a low of 22 kg in 1982. Amiro (2003a) notes that while restrictions

in the fishery may have reduced effort (and hence potentially catch) through time, these restrictions were implemented because of the scarcity of salmon. Additionally, the decrease in the commercial catch between the mid-1960's and the closure of the fishery by 1985 are consistent with the declines in abundance observed in the index rivers (see below) during the same time period.

Assessment of the status of iBoF salmon has typically been carried out using data from two index rivers (the Big Salmon and Stewiacke rivers), using electrofishing data from other rivers and adult salmon counts at a fishway on the Gaspereau River. A regional assessment process meeting on status of iBoF salmon was convened during 2003 (O'Boyle 2003) in support of an upcoming COSEWIC review of the listing. At this meeting, Gibson and colleagues reported declines in abundance of salmon of greater than 99% in the Stewiacke River (Gibson and Amiro 2003), and about 95% in the Big Salmon River (Gibson et al. 2003b) between the mid-1960's and 2002. Electrofishing in 44 rivers around the inner Bay of Fundy in 2002 indicated that the declines are widespread throughout the region, and that declines appear to be ongoing in rivers without LGB support (Gibson et al. 2003a). At present, abundance of adult salmon is monitored by counts at fish ladders on the Gaspereau River, and by dive counts and mark-recapture experiments on the Big Salmon River. In 2003, the number of salmon ascending the fish ladder at the White Rock dam on the Gaspereau River was seven, down from 102 in 1997 (Table 2.2). The number of adult salmon returning to the Big Salmon River in 2003, estimated by mark-recapture, was 21 (95% C.I.: 14.6 to 46.6 fish). Both these rivers receive LGB support.

Abundance in other rivers is inferred from electrofishing data. Electrofishing surveys in inner Bay of Fundy rivers from 2000 to 2003 are summarized by Gibson et al. (2003a, 2004). During 2002, an extensive electrofishing survey was undertaken to estimate the abundance of juvenile Atlantic salmon in iBoF rivers. During the survey, a total of 246 sites were electrofished in 48 rivers (Figure 2.2). Of 34 rivers without LGB support, fry were not found in 30 of these rivers and parr were absent in 22. Where salmon were present in rivers without LGB support, mean densities of fry and parr were very low. In New Brunswick iBoF rivers, mean densities of fry were less than 5.2 fish/100 m^2 and parr were less than 3.8 fish/100 m^2. In Nova Scotia iBoF rivers without LGB support, fry were totally absent and mean densities of parr were less than 7.1 fish/100 m^2 (and much lower in most rivers). During the 2003 survey, 112 sites were electrofished in 16 rivers. Salmon were not captured in five of ten rivers without LGB support and densities were low in the other five rivers. Densities are increasing in rivers with LGB support, but the box plots indicate that salmon densities remain lew in many parts of these rivers. Salmon were present at low densities in six rivers in 2000 in which salmon were not found during 2002 or 2003, indicating that river-specific extirpations are ongoing.

Presently, not all salmon spawning in iBoF rivers are of iBoF origin. Genetic analyses have revealed that the salmon parr captured in the Harrington River in 2002 have a high incidence of European alleles and are quite dissimilar from iBoF salmon, although their

origin is unknown. Additionally, some parr captured in the Upper Salmon River are of European origin and are likely aquaculture escapes (O'Reilly, personal communication[1]).

The presence of salmon in rivers with LGB support indicates that these rivers contain habitat capable of supporting salmon at least from the fry to the smolt stage. The number of smolt emigrating from the Big Salmon River (a LGB river) was estimated by mark-recapture during 2003 (Gibson et al. 2004). An estimated 9,191 smolt (95% C.I.: 7,761 to 11,178 smolt) emigrated from the Big Salmon River in 2003, including about 4,957 age-1 smolt that were released into the Big Salmon River as adipose-clipped age-0 parr in 2002 (in total, 34,000 age-0 parr were released in this river in 2002). The release of 78,000 adipose-clipped age-0 parr in 2001 resulted in an estimated 1,162 age-2 smolts in 2003. These results suggest that at least this river contains habitat capable of producing smolt. Additionally, electrofishing in several rivers with LGB support in which wild populations have been extirpated indicate that these rivers are able to support parr populations (Gibson et al. 2004).

2.3 Life history

Atlantic salmon have a rich and complicated life history, and an individual may follow a wide variety of different paths to contributing to the next generation. It has been shown that there is broad variation in life history both within and between populations throughout their geographic range (Gibson 1993, Fleming 1996, Hutchings and Jones 1998). As noted before, iBoF salmon populations differ from neighbouring regions in several ways. IBoF salmon usually enter rivers in the fall, and their abundance does not correlate strongly with the abundance of returning salmon in other regions (Amiro 2003a). The age structure of returning adults indicates a reproductive strategy that favors maturation after one sea-winter (referred to as 1SW salmon). Two sea-winter (2SW - salmon that mature after two winters at sea) adults are present but uncommon, and 3SW salmon are extremely rare (and possibly a stocking artifact). IBoF populations are therefore principally comprised of one sea-winter (1SW) and repeat-spawning 1SW salmon (Jessop 1986, Amiro 2003a). Tagging of wild and hatchery smolt indicated that salmon from iBoF rivers rarely migrate to the North Atlantic Ocean, and analysis of age data indicates that iBoF salmon have high survival between consecutive spawning years (Amiro et al. 2003). Within the iBoF, two subgroups have been identified. Populations originating in rivers within the Minas Basin are evolutionarily distinct from those in the Chignecto Bay and southward along the New Brunswick coast to the St. John River (Verspoor et al. 2002). Life history parameters and survival rates of salmon for rivers in the iBoF and many other regions are tabulated in Hutchings and Jones (1998) and Legault (in prep). A summary of the values gathered from the literature is presented in Table 2.3.

[1] Dr. Patrick O'Reilly. Diadromous Fish Division, Department of Fisheries and Oceans, Dartmouth, NS.

2.4 Habitat requirements

2.4.1 Freshwater

Salmon require several different habitats to complete a life cycle, and as a salmon grows to maturity, habitat requirements change. Successfully linking habitat types is an important determinate of growth, survival and lifetime reproductive success. Gibson (1993) identified three major freshwater habitat types i) feeding habitat, ii) winter habitat, and iii) spawning habitat. Armstrong et al. (2003) separated the habitat requirements of early life stages into nursery and rearing habitat, and added to the list habitat that was used during up-river migration. The quality of habitat can be affected by 1) seasonal temperatures, 2) stream discharge, 3) water chemistry (e.g. pH, nutrient levels, oxygen concentration), 4) turbidity, 5) invertebrate abundance, and 6) physical perturbations (e.g. impoundments, deforestation), as well as many other factors (Gibson 1993, Armstrong et al. 2003). Amiro (1993) and Amiro et al. (2003) found stream gradient to be a good indicator of habitat quality, with optimal gradients ranging from 0.5 to 1.5%. The model HABSCORE combines many abiotic and biotic factors and successfully predicts habitat quality in several UK rivers (Milner et al. 1998). Armstrong et al. (2003) stressed the importance of identifying habitat factors that could increase overall production, otherwise errors could be made in manipulating already abundant habitat or by increasing the abundance of a life stage that is only limited later by some other factor.

2.4.2 Marine

Much less is known about the habitat requirements of salmon at sea. The paucity of information is due, in part, to the difficulty in collecting data on salmon at sea. Salmon catches in Iceland were significantly correlated with hydrography, primary production, standing crop of zooplankton, and the distribution and abundance of forage fish (Scarnecchia 1984). Sea surface temperature has been correlated with the recreational catches of salmon in the Bay of Fundy (Ritter 1989), the abundance of salmon off West Greenland (Reddin and Shearer 1987), and the return rates of grilse to Iceland (Scarnecchia 1984).

Few tags applied to iBoF salmon have been returned from areas outside the Bay of Fundy, indicating that iBoF salmon may not typically migrate far beyond the Bay of Fundy (Jessop 1976, Amiro et al. 2003). Marine survival has decreased rapidly in the iBoF as well as throughout much of eastern Canada (Amiro 2003a, Chaput et al. 2003), and is currently much lower than in European populations (Ó Maoiléidigh et al. 2003). Marine survival decreased from 4.5% in the 1970's to less than 1% in the 1990's in the Stewiacke River (Ritter 1989, Amiro and Jefferson 1996). Similar decreases have been observed in the Big Salmon River where the estimated survival of the 2001 smolt year class to returning 1SW salmon was about 0.7% (Gibson et al. 2004).

2.4.3 Habitat maps

Amiro et al. (2003) reviewed the literature on habitat requirements for Atlantic salmon by life stage. Amiro (1993) estimated the productive capacity of habitat using remote-sensed habitat data (gradient, stream width and distance from the mouth measured from

ortho-photo maps and aerial photographs) and historical distributions (parr densities determined by electrofishing) and found that gradient was a good predictor of parr density. Amiro et al. (2003) report a summary of remote-sensed measurements of gradient, width, and length of stream reaches from 22 iBoF rivers. We have subsequently digitized their data. Using a heads-up digitizing method, we edited the 1:50,000 Coastal Map Series stream segments to match the stream segments measured on the orthophoto maps, and assigned habitat attribute data (gradient and stream width) to each stream segment. The extent of the habitat mapping relative to the total available within the inner Bay is shown in Figure 2.3. The habitat maps are shown in Figures 2.4 and 2.5. Habitat within the south part of the Minas Basin is typically of lower gradient, although a lot of habitat is present within the 0.5 to 1.5 % gradient category shown to be of high preference (Amiro et al. 2003). To the north, a large proportion of the habitat is in these high preference categories. As expected, the widths of the rivers decrease as one moves upstream from the mouth of the river (Figure 2.5). The overall productive capacity of these rivers, estimated using the amount of habitat available by gradient category, is available in Amiro et al. (2003).

Amiro et al. (2003) also mapped marine habitat quality based on monthly sea surface temperature.

3.0 Critical habitat evaluation

We approached the effectiveness of a critical habitat designation by evaluating the relationship between habitat quantity and quality and the survival and recovery of iBoF salmon. We began by asking whether or not a critical habitat designation would aid in the survival or recovery of iBoF salmon. We examined the effects of habitat quantity and quality at the watershed scale using a population viability analysis (PVA) for a population in an individual river. The model is not spatially explicit, and in the event that survival and recovery are sensitive to the quantity and quality of habitat, identification of critical areas and incorporation of spatial structure would be the next step in the analysis.

The objectives of our analyses were to 1) determine if the probability of persistence of iBoF salmon is sensitive to changes in habitat quantity and quality, and 2) to determine the relative influence of other life history parameters on the probability of persistence.

3.1 Introduction

PVA is an important tool which can be used to identify critical habitat. In PVA, a population dynamics model is used to determine how the probability of persistence is affected by current conditions and future perturbations (Beissinger and McCullough 2002). The goals of a PVA are to 1) determine the current viability of a population, 2) identify threats to persistence, and 3) provide a defensible structure for management and legal action. Typically, there are several other benefits of PVA such as identifying information gaps, and directing future research. A disadvantage is that PVA is data intensive and few species meet the minimum data requirements.

With sufficient data, vital rates such as growth, survival and reproduction can be linked to habitat features (Hayes et al. 1996). A PVA can then provide quantitative estimates of how the probability of persistence (preferably including uncertainty in parameter estimates) changes with habitat quantity and quality.

We analyzed the viability of iBoF salmon by building a life history based, age-structured population model. The structure of the model is similar to other Atlantic salmon population models (Evans and Dempson 1986, Korman et al. 1994), but differs in where density dependence occurs (between age-0 and age-1 parr; see below). To develop and parameterize our model, we drew on several studies of salmon in two iBoF rivers, the Big Salmon River and Stewiacke River (Gibson et al. 2003a, Gibson et al. 2003b). We then used data from the Big Salmon River to derive parameter estimates for the life history model using maximum likelihood. A key purpose for the statistical analysis was to determine which life history parameters had changed, and when. We then used the resulting model output for deterministic and stochastic analyses of population viability that are used to determine whether population persistence and recovery are sensitive to either the quality or quantity of habitat available to the population.

Under the SARA, critical habitat is defined as the habitat that is needed for population survival or recovery, and as a result, recovery targets are needed for the analysis. At present, recovery targets have not been established for iBoF salmon, so in this document we use two methods for choosing targets.

The following sections proceed through a review of potential recovery targets and estimation of minimum effective population size (section 3.2), the development of a life history based, population dynamics model (section 3.3), parameter estimation for the model using maximum likelihood (section 3.4), a deterministic analysis of the model output to determine whether equilibrium population size and population growth are sensitive to habitat quantity and quality (section 3.5), and a stochastic analysis of the model output to determine the sensitivity of the results to the input parameters and to determine how the probability of persistence is affected by changes in habitat quantity and quality (section 3.6).

3.2 Recovery targets

Recovery targets have not been established for iBoF Atlantic salmon populations but are necessary to evaluate the minimum amount of habitat required for recovery. For the purposes of our analyses, we considered that either the conservation limits established for fisheries management could be used as recovery targets, or that recovery targets could be established by estimating the minimum viable population size needed to maintain genetic diversity.

Marshall et al. (1992) estimated spawning requirements for three iBoF rivers: the Shubenacadie (350 1SW and 130 MSW salmon), the Stewiacke (800 1SW and 310 MSW salmon), and the Big Salmon (280 1SW and 420 MSW salmon). These requirements have been used as reference points for fisheries management. O'Connell et al. (1997) reported similar conservation limits based on habitat area for 26 inner Bay of Fundy

rivers. Their values differ slightly from those of Marshall et al.: Shubenacadie (610 small and 228 large salmon), the Stewiacke (772 small and 289 large salmon), and the Big Salmon (280 small and 420 large salmon) rivers. These values are potential recovery targets.

An alternative method for establishing recovery targets is to identify the minimum population size needed to maintain genetic diversity. Since not all individuals are sucessful in producing offspring, it is necessary to estimate the effective population size (N_e) which is the number of reproducing individuals in an ideal population that would lose genetic variation due to drift or inbreeding at the same rate as the number of reproducing adults in the real population under consideration. Genetic diversity is lost when the effective populations size is low, and extreme events where the population size remains low for several generations are referred to as bottlenecks. Lande and Barrowclough (1987) showed that an effective population size of approximate 500 individuals can maintain most genetic variability. In Pacific salmon, a minimum of 100 breeding individuals may be necessary to reduce the rate at which genetic variability is lost (Waples 1990). Recently, Elliott and Reilly (2003) found that an effective breeding population of 80 – 90 individuals (originally from the River Phillip, Nova Scotia) was sufficient to maintain most of the genetic variability in Atlantic salmon populations introduced in Australia and Tasmania.

Relatively few attempts have been made to estimate the effective population size N_e for Atlantic salmon. Overlapping generations, an iteroparous life history, and the potential for straying makes the estimation of N_e difficult. However, several studies have estimated N_e and N_e / N_{census} ratios for other salmonids (Table 3.1). The average of the lower and upper limits of N_e / N_{census} ratios across taxa and studies in Table 3 give a range from 0.26 to 0.88. These values can only be considered a coarse approximation of the range of N_e / N_{census} ratio for Atlantic salmon. In fact, the N_e / N_{census} ratio for Atlantic salmon would tend to be larger than estimates for other salmonids because of the contribution of sexually mature male parr (Jones and Hutchings 2001, 2002). If we use the range of 0.26 – 0.88 and assume that a minimum of 80 – 100 individuals are necessary to maintain genetic variability, then the minimum total population size should be between 91 – 385. If we use Lande and Barrowclough's (1987) more conservative estimate of a minimum effective population size of 500 indviduals, then minimum census population size should be between 568 – 1,923 individuals. These values assume a closed population. If straying exists between rivers, the minimum census population size required to maintain genetic diversity would be lower.

3.3 Atlantic salmon life history model

In this section, we explain the life history model used to evaluate whether a critical habitat designation would be beneficial for Atlantic salmon. A key aspect of any demographic model is the timing and extent of density dependence. In Section 3.3.1, we evaluate when density dependence occurs in the freshwater life stages, and in Section 3.3.2, we develop the model equations.

3.3.1 Density dependence

An important part of population modelling is to determine the timing and extent of density dependence in the population. It is thought that most of the density dependence in salmon populations occurs in early life stages during a 'critical period' (Elliott 2001). We used electrofishing data from two iBoF rivers, the Stewiacke and the Big Salmon, to test for density dependence in fresh water between the egg stage and parr at age-2. We tested for density dependence by comparing the fits of a linear (density independent) model (forced through the origin) with the Beverton-Holt spawner-recruit (density dependent) model.

The Beverton-Holt and Ricker models are the most commonly used two parameter spawner-recruit models (Hilborn and Walters 1992). These models differ fundamentally in their assumptions of the underlying biology, the latter showing a decline in recruitment at higher spawner abundance, a phenomenon known as overcompensation. Myers et al. (1995a) fit both Beverton-Holt and Ricker models to Atlantic salmon spawner-recruit data. Examination of the log-likelihoods reported by Myers et al. (1995a) indicates that the Beverton-Holt model provides a consistently better fit to Atlantic salmon data than did the Ricker model. The Beverton-Holt spawner-recruit model gives the number of recruits, R, as a function of the number of spawners, S:

$$R = \frac{\alpha S}{1 + (\alpha S / R_0)}.$$

Here, α is the slope at the origin, and in the deterministic model is the maximum rate at which spawners can produce recruits at low population sizes (Myers et al. 1999) and R_0 is the asymptotic recruitment level. As S approaches infinity, R_0 is the limit approached by R (Beverton-Holt models are often written in terms of the half saturation constant, K, which is related to R_0 by: $R_0 = \alpha K$). Parameter estimates for each population were obtained using maximum likelihood assuming a lognormal error structure for recruitment (Myers et al. 1995a). Denoting the Beverton-Holt spawner-recruit function as $g(s_i)$, the log-likelihood is given by:

$$\ell(\alpha, R_0, \sigma) = -n \log \sigma \sqrt{2\pi} - \sum \log r_i - \frac{1}{2\sigma^2} \sum \log\left(\frac{r_i}{g(s_i)} \right)^2$$

where s_i and r_i are the observed spawner biomass and recruitment data, σ is the shape parameter and n is the number of paired spawner-recruit observations. When testing for density dependence between two age classes, we substituted the abundance of the younger age class for the spawner abundance and the abundance in the older age class for the number of recruits.

Parr density (number per $100m^2$) was recorded at 27 to 44 sites on the Stewiacke River from 1984 to 2002, and at three to seven sites on the Big Salmon River intermittently (1968, 1970-1973, 1989-2002). For each river, we compare the mean densities in each

age class in consecutive years to test for density dependence. Years when the densities were potentially affected by stocking were not included in the analysis. In the seven comparisons (density dependent versus density independent) that were made (Figure 3.1), the addition of a second parameter for density dependence was only statistically significant in one case (Table 3.2). This case was between age-0 and age-1 for the Big Salmon River salmon. We noted that in two cases the resulting survival estimates exceeded one, a biological impossibility. Both instances involved densities of age-0 parr that may have been underestimated relative to age-1 and older parr during the electrofishing surveys. This bias would not affect conclusions drawn about the timing of density dependence as long as the bias was consistent from year to year.

3.3.2 Life history model

In order for population regulation to occur, density dependence must occur (Royama 1992). Based on the above analysis, we set up our model with density dependence between age-0 and age-1. We assumed that all parr smoltified by age-4, an assumption consistent with the observed ages of smolt in the Big Salmon River (Jessop 1975, Gibson et al. 2004). We also assumed that post-smolt spend no more than two years at sea before maturing. Finally we assumed that adults may spawn up to a maximum of five times in their life. Within the inner Bay of Fundy, the vast majority of salmon repeat spawn annually after maturity (Jessop 1986). We did not include the alternate year repeat spawning (because it is very rare) or precocious parr life history strategies (because egg and not sperm production tends to be limiting) within our model.

Let the subscripts t index the year, a age, s sex ("m" or "f"), c the number of winters a smolt remains at sea prior to returning to spawn for the first time, p the number of times a fish has previously spawned. The number of fish entering the river to spawn is denoted as $N_{t,s,a,c,p}$. For simplicity, we assumed that life history events such as hatching, smolt emigration and maturity occur on May 1st, with the exception of spawning which occurs during the fall. Age-0 refers to fish in their first year of life (from hatch to May 1st of the following year). This age category includes a life stage sometimes called "fry". However, we refer to all fish age-0 to age-2 as parr, rather than separating the first year after hatch into two life stages. The term "smolt" refers to immature fish that are migrating to sea; and immature fish at sea are termed "post-smolt". The term "adult" refers to fish that have migrated to sea as smolt and are returning to the river to spawn, i.e are sexually mature. We distinguish between mortality at different life stages or locations using superscripts (e.g. M^{Sea} or M^{Adult}), and use subscripts to denote different rates for age or life history classes and years.

1. Egg production:

The number of eggs produced in the year t, Q_t, is a function of the number of returning females that survive to spawn, $E_{t,f,a,c,p}$, and the class-specific female fecundity, f_c (small or large). Spawning occurs during the fall.

$$Q_t = \left(\sum_{a,c,p} E_{t,1,a,c,p} f_{t,c} \right).$$

2. Production of age-0 parr in freshwater:
Let $P_{t+1,0}$ be the number of age-0 parr in year t+1. The relationship between the number of age-0 parr in the spring and egg production during the previous fall is:

$$P_{t,0} = Q_{t-1}(1 - M^{\text{Egg}}),$$

where M^{Egg} is the combined mortality from time of egg deposition to the end of the yolk-sac larval stage. M^{Egg} is assumed to be density independent.

3. Production of age-1 and older parr:
We assumed that mortality between age-0 and age-1 is density-dependent and that the Beverton-Holt function describes the nature of this density dependence. In this model, R_0 is the asymptotic density (number per 100 m^2), and h is the number of 100 m^2 habitat units available to the population. Alpha (α) is the maximum survival rate between age-0 and age-1, which occurs at low population size where the slope of the Beverton-Holt function is steepest. We define j_a as vector containing the age-specific probability that a parr develops into a smolt at that age. The number of age-1 parr is given by:

$$P_{t,1} = \frac{\alpha P_{t-1,0}}{1 + \frac{\alpha P_{t-1,0}}{R_0 h}} (1 - j_1)$$

The number of age-2 and older parr is determined by the number of parr in the cohort in the previous year, the annual mortality rate of parr, M^{Parr} (assumed density independent), and the probability of smoltification:

$$P_{t,a} = (P_{t-1,a-1})(1 - M^{\text{Parr}})(1 - j_a).$$

4. Production of smolt and immature salmon at sea:
At this point, the model keeps track of the abundance of males and females separately. We denote the number of post-smolt in year t, of sex s, age a, in sea-age class c as $S_{t,s,a,c}$, the probability that a post-smolt in sea age class c matures as m_c, the mortality of immature fish at sea as M^{Sea}, and the sex ratio in the smolt year class as v_s. The number of post-smolt is given by two equations:

$$S_{t,s,a,c} = \begin{cases} P_{t-1,a-1}(1 - M^{\text{Parr}})(j_a)v_s & \text{if } c = 0 \\ S_{t-1,s,a-1,c-1}(1 - M^{\text{Sea}})(1 - m_c) & \text{if } c > 0 \end{cases}.$$

5. Production of mature adults:
The number of fish returning to the river to spawn, $N_{t,s,a,c,p}$, is given by two equations, depending whether the fish is a first time spawner ($p = 0$), or a repeat spawner ($p > 0$). M^{Adult} is post-spawning natural adult mortality and F_t is the instantaneous rate of fishing mortality in the river.

$$N_{t,s,a,c,p} = \begin{cases} S_{t-1,s,a-1,c}(1-M^{\text{Sea}})(m_c) & \text{if } p=0 \\ N_{t-1,s,a-1,c,p-1}(1-M^{\text{Adult}})e^{-F_{t-1}} & \text{if } p>0 \end{cases}.$$

6. Spawning escapement is the number of returning salmon not harvested by the fishery.

$$E_{t,s,a,c,p} = (N_{t,s,a,c,p})e^{-F_t}$$

These fish produce eggs in year t thereby closing the life cycle (returning to step 1).

3.4 Statistical modeling

A fundamental question in recovery planning for endangered species is to determine which demographic parameters changed (and when) leading to a population that is in danger of extinction. In this section, we present an analysis of data for one inner Bay of Fundy salmon population to estimate carrying capacity, stage specific survival rates and an analysis of when and where (the freshwater or marine environment) these rates changed. We use data for the Big Salmon River salmon from the time period 1964 to 2003 for the analysis.

Gibson and Amiro (2003) and Gibson et al. (2003b) use a statistical, index based model to estimate abundance of Atlantic salmon in the Stewiacke and Big Salmon rivers from the early 1960's to 2002. Here, we adapt their approach to obtain population-specific parameter estimates for the model presented in the previous section. When all life stages are considered, more data spanning longer time periods exist for the Big Salmon River than for any other iBoF salmon populations. We focus on this population for this reason. Gibson et al. (2003b) used recreational fishery catch and effort data, counts of adults at a counting fence, counts of adults obtained from shoreline observation and dive surveys, redd counts and juvenile electrofishing data to estimate the number of adults returning to the river annually. Here, we add smolt counts at a counting fence, mark-recapture estimates of the number of emigrating smolt, and age-frequency data for both the emigrating smolt and returning adults. None of the data series span the full time period from 1964 to 2002. The time series available for each data set are shown in Table 3.3.

Following the approach of Gibson et al. (2003b), we adapted the life history model (Section 3.3.2) to make predictions corresponding to the observed data points. This adaptation involved adding equations to the model to make the predictions of the observed data and adding a component so that model parameters (life history and sampling) could be estimated using maximum likelihood. These components of the

model are shown in Table 3.4. Numbers in brackets in the following text refer to the equation numbers in this table.

3.4.1 Linking the life history model to data

The recreational catch is reported as the number of large and small salmon taken annually in the recreational fishery. We assumed all fish captured were removed from the population. We also assumed that all first time spawning 1SW salmon were small, and all repeat spawning 1SW and all 2SW salmon were large (1). While this assumption may lead to an over-estimate of the number of large salmon, we also estimated the proportion of 1SW salmon that were spawning for a second time that were in the small group, but this proportion was always less than 1%. As a result we dropped this component of the model. The catch in each year and size group (g), $C_{t,g}$, is related to $N_{t,g}$ through the instantaneous rate of fishing mortality for each size group and year, denoted $F_{t,g}$ (2). We assume that $F_{t,g}$ is a function of the fishing effort in year t, f_t, and is related through the catchability coefficient, q_g (3). The fence count in year t and size group g, $Fence_{t,g}$, corrected for the catch downstream of the fence, equals to the number of fish returning to the river in each size category and each year (4). The redd count in year t, $Redd_t$, is assumed to be a function of $E_{t,g}$ and the "observability" coefficient for redds, q_{redd} (5). During estimation, q_{redd} was not bounded at less than one to allow for the possibility that a fish might dig more than one redd, or for the possibility that redds might be misidentified. The shore and dive counts in year t, $swim_t$, are similarly related to $E_{t,g}$ through an "observability" coefficient for shore and dive counts, q_{swim} (6).

Observations in the electrofishing data that may have been influenced by the release of captive-reared juveniles were not included in the analysis. At present, we have not found data that allows separation of captive-reared and wild origin smolt and adults in the earlier time periods. Jessop (1975) reports that returns of tagged, captive-reared smolts that were released during 1968 and 1969 were extremely low, although this could be a tagging effect rather than stocking effect (Jessop 1986). Most smolt released into the Big Salmon River between 1964 and 1969 were of Restigouche River or Miramichi River origin (Gibson et al. 2003c), which might also reduce return rates. During 1994 and 1995, the 397 and 227 captive-reared small salmon released into the Big Salmon River were added to the spawning escapement when calculating egg deposition.

3.4.2 Parameter estimation

Parameter estimates were obtained by minimizing an objective function (*O.F.V.*) that is the sum of the negative log likelihoods (Quinn and Deriso 1999) for the catch (ℓ_{catch}), the fence counts (ℓ_{fence}), the redd counts (ℓ_{redd}), shore and dive counts (ℓ_{swim}), the juvenile electrofishing data ($\ell_{electro}$), the adult age frequency data (ℓ_{age}^{adult}) and the smolt age-frequency data (ℓ_{age}^{smolt}). We used lognormal error structures (Myers et al. 1995a) for all likelihoods except the age frequency data, for which multinomial likelihoods were used. Observed values are superscripted with "obs" (equations 8 to 12 in Table 3.4). In these equations, n is the sample size for the corresponding data set and $\sigma_{\cdot}$ is the corresponding

shape parameter (for a lognormal distribution, σ is the standard deviation of a normal distribution prior to exponentiation). In the two equations for the multinomial likelihoods (13 and 14), $n_{w,t}$ is the number of organisms of life stage w (smolt or adult) that were sampled in year t, r is the number of age categories, $x_{w,t,r}$ is the observed number of organisms in category r in the sample taken in year t, and $p_{w,t,r}$ is the corresponding predicted proportion.

Gibson et al. (2003b) had difficulty estimating the σ's for all model components. Following their approach, we used the average σ's obtained by Myers et al. (1995a) for the spawner-recruit relationships for 15 populations and recruitment age categories for Atlantic salmon. For a recruitment age of 1, σ averaged 0.330 (n = 4; range: 0.293 to 0.402). Models were also fit to single data sets for recruitment ages of 0 and 2, for which σ was estimated as 0.334 and 0.581 respectively. These estimates were similar to the estimated σ's when smolt was used as the recruitment category (mean=0.329; n=5; range: 0.206 to 0.440). Based on these analyses, we set σ_a equal to 0.33 for the three electrofishing age categories. σ_{fence} was set equal to 0.1 to reflect a higher degree of certainty about the fence count data. In an analysis of index data for Stewiacke River salmon, Gibson and Amiro (2003) estimated $\sigma_{catch\,s}$ and $\sigma_{catch\,1}$ to be 0.91 and 1.0 respectively. We set $\sigma_{catch\,s}$ and $\sigma_{catch\,1}$ equal to 1.0 based on their analyses. σ_{redd} and σ_{swim} were set equal to 0.5 to reflect a less variable process than the fishing component of the model, but greater variability than in the fence counts.

3.4.3 Model formulations

We set up the model to estimate the number of fish in each life stage and age category during the first year (1964), the survival rates and the life stage transition probabilities (probability of smolting, probability of maturing). The number of fish in the first year was estimated by first estimating egg deposition from 1959 to1964. These values were used to fill in the abundance arrays using the estimated survival and transition probabilities up to age-5. The remaining age classes in the first year were filled in by decrementing abundance by 0.5. This procedure has only a very small effect on abundance in the first year and reduced the number of parameters that has to be estimated by the model. After initialization, abundance was projected forward using the life history parameters estimated in the model. Estimated life history parameters were: mortality from egg to fry (M^{Egg}), the Beverton-Holt spawner-recruit parameters (α and R_0) used to model survival from age-0 to age-1, the probabilities of developing into a smolt at ages 2 and 3: (j_2 and j_3), annual mortality of parr after age-1 (M^{Parr}), annual mortality of immature salmon at sea (M^{Sea}) the probability of maturing as a 1SW salmon (m_1) and post-spawning adult mortality (M^{Adult}). Other estimated parameters were the catchability or observability coefficients: q_g (two parameters), q_{redd} (one parameter) and q_{swim} (one parameter), as well as the number of habitat units available to the population h. This last value is used to scale from the densities of juveniles obtained by electrofishing to the number of juveniles present in the population.

We set up the model three ways. In the "base" model, age and stage specific abundance was projected forward through time using life history parameters that were assumed constant through time. In the "marine" model, we assumed that the life history parameters relating to the marine life stages (M^{Sea}, M^{Adult} and m_1) changed at some point in time. In the "freshwater" model, life history parameters relating to survival in freshwater juvenile life stages (M^{Egg}, α, R_0 and M^{Parr}) changed at some point in time. Step functions were used in the latter two models (parameter values changed abruptly at some point in time, but were constant otherwise). We chose the break year for the step functions by fitting the model with different break years and comparing the value of the minimized objective function over these model runs.

The model was programmed using AD Model Builder (Fournier 1996). AD Model Builder (ADMB) uses the C++ auto-differentiation library for rapid fitting of complex non-linear models, has Bayesian and profile likelihood capabilities, and is designed specifically for fitting these types of models.

3.4.4 Results

Comparison of the objective function value with the break year (Figure 3.2) for the marine model indicates that, relative to other years, a change in the values of life history parameters in marine environment at 1970 is probable. This year roughly coincided with the cessation of stocking of Miramichi River and Restigouche River progeny (stocks that typically mature later and are expected to have different survival) into the Big Salmon River and was not chosen as the break year for this reason. Years close to 1970 are likely influenced by these events. After this time period, the next most probable year is 1990, and this year was chosen as the break year as a result.

The fit of the three models to the recreational catch data is similar (Figure 3.3), although the "marine" model provided slightly higher estimates of the catch. None of the models captured the variability in the catch well, suggesting that factors other than changing spawner abundance as a result of fishing is contributing to this variability (the low magnitude of the predicted catch is due in part to the assumed lognormal errors). Estimated exploitation rates are also similar between the models (Figure 3.3). The predicted juvenile densities did vary between models with the "freshwater" model providing estimates of age-1 density that were less than the other models during the earlier time period, and higher than the other models in the later time period (Figure 3.4). The "base" and "freshwater" models both overestimate the age-0 and age-1 densities in the earlier time period.

Because the "base" model goes to equilibrium earlier than the other models (in the absence of perturbations such as fishing or stocking), the fit through the redd and dive count data is essentially flat with a slight increase as a result of the adult releases in the early 1990's (Figure 3.5). The other two models had not yet reached equilibrium during the 1990's and show declining trends during these years. Consequently, these models captured the pattern in the data more closely.

All three models overestimated smolt abundance in the early time period and underestimated smolt abundance in the later time period (Figure 3.6). This is possibly a stocking effect if progeny stocked in the early period contributed to the returning number of adults and if the stocking of fry in the later time period contributed to the observed number of smolt. The "freshwater" model overestimates the observed number of smolt in the pre-1970 time period by a factor of three to five.

All three models predict declines in the number of returns from 1964 to 2002 (Figure 3.7). The base model approaches an equilibrium in the 1990's whereas ongoing declines through this period are predicted by the other models. None of the models predict the observed increase in abundance from 1964 to 1967, an increase that is possibly due to stocking prior to and during this time period.

While the patterns predicted by the models are roughly similar, an important difference is that the models that allowed life history parameters to differ between the two time periods predict ongoing declines, whereas the base model reaches an equilibrium population size during the period under study. The former pattern (ongoing declines) is much more consistent with observations on the Big Salmon and other rivers in the inner Bay of Fundy (Gibson and Amiro 2003, Gibson et al. 2003a, 2003b). The mechanism contributing to the declines is markedly different between the "freshwater" and "marine" models. In the "freshwater" model, the estimated asymptotic level for age-1 parr goes to a poorly estimated and unrealistically high value (559 parr per $100m^2$), followed by very high mortality in freshwater after age 1. The estimated survival from age-0 to age-1 (0.909) predicted by this model for the later time period is also unrealistically high, and results in a model where abundance is nearly independent of spawner abundance. In contrast, the "marine" model provides estimates that are biologically reasonable for both time periods and are consistent with the observed rates. This model predicts that mortality of immature salmon at sea changed from an average of 0.829 to 0.970 between the two time periods, while post-spawning adult mortality changed from 0.495 to 0.643 and the probability of maturing as a one sea-winter salmon increased from 0.278 to 0.840. Because the estimates are more biologically realistic, and because this model more closely predicts the smolt data, our preference is for this model. The estimates of life history parameters produced by this model are used in the remaining analyses.

We acknowledge here that this model does not capture all the demographic changes undergone by this population. These changes did not occur instantaneously in 1990, and likely are more gradual and ongoing. For example, Gibson et al. (2004) estimated a return rate for 1SW Big Salmon River salmon of 0.3%, a value lower than that predicted by the model. Hence, the viability of the population is probably overestimated if the post-1990 parameter estimates are assumed indicative of the present state. However, the formulation used herein does provide information about whether changes occurred in the freshwater and marine environments, the timing of the changes and the extent to which life history parameters have changed.

3.5 *Deterministic analyses*

In this section, our goal is to determine how equilibrium population size and population growth rate vary with habitat quantity and quality, given the life history parameter estimates obtained in the previous section.

The lifetime reproductive rate (λ, defined as the number of eggs produced per egg throughout the organism's life) of an Atlantic salmon can be calculated from the life history model by multiplying the number of eggs per recruit (EPR) by the number of eggs that survive to become a recruit (RPE). In this analysis, we consider a smolt as a recruit, and consequently make a break in the life cycle between the early freshwater stages and the marine phase. The number of eggs produced by a smolt throughout its life is given by:

$$EPR = \sum_{c=1}^{2} Q_c \,, \qquad \text{where}$$

$$Q_1 = (1 - M^{\text{Sea}})(m_1) f_1 + \sum_{0}^{\max p} (1 - M^{\text{Adult}})^p f_2 \,,$$

$$Q_2 = (1 - M^{\text{Sea}})^c (1 - m_1) \sum_{0}^{\max p} (1 - M^{\text{Adult}})^p f_2 \,,$$

where c isthe number of years spent at sea prior to maturity, M^{Sea} the annual mortality of immature salmon at sea, m_1 the probability of maturing after one winter at sea, f_c the fecundity of first-time spawning 1SW (f_1) or older salmon (f_2), p the number of previous spawnings, and M^{Adult} is the adult annual mortality rate. Because all fisheries are closed, fishing mortality is not included in the model.

Since we assume that density dependence occurs between age-0 and age-1 (and also that survival from egg to age-0 is density independent), the number of age-1 parr per egg also follows a Beverton-Holt relationship (parameter definitions as in Section 3.2.2):

$$P_1 = \frac{\alpha}{1 + \dfrac{\alpha Q}{R_0 h}} (1 - M^{\text{Egg}}) \,.$$

The number of recruits (smolt) per egg is then calculated from the number of age-1 parr per egg times the number of smolt produced per age-1 parr:

$$RPE = P_1 \sum_{a=1}^{4} (1 - M^{\text{Parr}}) \prod_{k=1}^{k=a-1} (1 - j_k) j_a \,.$$

The lifetime reproductive rate at a given population size (number of eggs) is then:

$$\lambda \mid Q = EPR \cdot RPE \mid Q .$$

Here, the lifetime reproductive rate is a density dependent function of the number of organisms in the cohort, determined by Q.

We found the equilibrium population sizes (Q^*) by finding the number of eggs such that the rate at which smolt produce eggs equals the rate at which eggs produce smolt given the above relationships.

We determined the sensitivity of λ and Q^* to habitat quantity and quality by varying h and α at three population sizes as noted before: current, recovery target, and past. We then examined the sensitivitiy of lifetime reproductive rate (λ) to changes in mortality of immature fish at sea, habitat amount and quality. We also examined the effects of changing habitat amount on equilibrium population size under past (1964-1989) and recent conditions (1990-2003). Life history parameter estimates obtained from the "marine" model for salmon of the Big Salmon River in Section 3.5 (Table 3.5) were used for this analysis. Constants and dimensioning parameters for the life stage arrays are listed in Table 3.6. Since recovery targets for iBoF salmon have not been established, we simulate the effects of habitat change at three levels of population abundance: current (2002: c.10 adults), a hypothetical recovery target (c.500 adults) selected based on the analyses in Section 3.2, and past (1964 - 1989: c.3,000 adults).

3.5.1 Results

Equilibrium population size was calculated using the life history parameters estimated for the past (1964 – 1989) and present (1990 – 2003) conditions. Calculations were made assuming no change in the number of habitat units, assuming the number of available habitat units is doubled, and assuming the number of available habitat units is halved. Under a higher marine survival scenario (past conditions), the equilibrium population size is very sensitive to the amount of freshwater habitat available (Figure 3.8). Under present conditions (low marine survival), equilibrium population size is not very sensitive to the amount of freshwater habitat because the resulting freshwater juvenile densities are low enough that density dependence is low. Thus, because space is not limiting under these conditions, increasing habitat availability in freshwater should have little effect on the level of density dependent mortality and population size. Past abundances cannot realistically be achieved under present marine mortality rates by manipulating the amount of freshwater habitat.

We found that the lifetime reproductive rate, λ, was sensitive to amount of freshwater habitat (Figure 3.9). Under this scenario, if population size is increased (500 and 3,000 adult fish scenarios), say by the release of captive-reared fish, the population size will decrease ($\lambda<1$) and the rate of decrease increases with habitat loss. Increases in habitat quality (modeled here through density-independent age-0 to age-1 survival) have the potential to increase the lifetime reproductive rate (Figure 3.9). At low population sizes the lifetime reproductive rate is more sensitive to habitat quality than at higher population sizes.

The relationships between the lifetime reproductive rate and habitat quantity and quality depend on the mortality rate of post-smolt at sea as well as population size (Figure 3.10). At high levels of mortality, the lifetime reproductive rate is not very sensitive to freshwater habitat loss, and populations simply are not viable. If marine survival increases, the rate of population growth also increases, and under these conditions populations will rebuild more rapidly in rivers with more habitat. The lifetime reproductive rate is also sensitive to habitat quality (Figure 3.10). At high levels of marine mortality, increasing density independent survival (age-0 to age-1) by increasing habitat quality cannot offset the high marine mortality without changing other parameter values as well (e.g. M^{Egg} or M^{Parr}). These analyses also indicate that habitat is required for populations to recover. For example, to maintain a population size of 500 adult fish at a marine mortality rate of 0.85 (and all other model parameters as specified in Tables 3.5 and 3.6), about 500 habitat units are required (Figure 3.10).

3.6 Stochastic analysis

We examined the population viability of iBoF salmon using a stochastic population model. We added variability to all survival rates and stage transitions (maturity and smoltification probabilities) and examined the sensitivity of the population (in terms of persistence) to changes in habitat quantity, quality and the assumed survival rates. Myers et al. (1995a) fit spawner-recruit models to data for several North American salmon populations. In their analyses, when estimated using a Beverton-Holt spawner-recruit model with a lognormal error structure, σ (the standard deviation of a normal distribution prior to exponentiation) ranged from 0.09 to 0.52 and averaged 0.32 (Table 3.7). In our population viability analyses, we therefore assumed sigma = 0.3 for the lognormal variability around the Beverton-Holt relationship describing the density dependent production of age-1 parr by age-0 parr. At present, we do not know the variability of other survival rates or transition probabilities for iBoF salmon. All other rates and transition probabilities in our model are proportions. We added variability to these values by first logit transforming the estimated proportions (this maps the interval [0,1] to the real line), then drawing a random number from a normal distribution with the mean determined in the previous step, and an assumed standard deviation of 0.5. The resulting random number was then back-transformed to obtain a proportion with random error. Samples of the probability distributions used to draw random numbers are shown in Figure 3.11. Fecundities and dimensioning parameters for the life stage arrays (e.g. minimum age, maximum age) are provided in Table 3.6. For most simulations, the parameter values are those estimated for the 1990's using the statistical model (Table 3.5), with exceptions occurring when the sensitivity of the results to a specific parameter is being analyzed.

3.6.1 Results

In the results that follow, we begin by showing an example of a single population simulation from the PVA. We then show summaries of multiple iterations of the PVA at different rates of marine survival. We then use the model to evaluate whether population

persistence is sensitive to the amount of available habitat. Finally, we evaluate the sensitivity of the conclusions to the parameter values used in this analysis.

A typical single run of the stochastic population model, with random variability added as described above and a starting population size of 15 small and 15 large salmon, is shown in Figure 3.12. The population size decreases rapidly and is extinct in about 13 years.

Summaries of 1,000 runs of the PVA model for three rates of annual mortality of immature fish at sea are shown in Figure 3.13 (starting population size = 30 adults) and Figure 3.14 (starting population size = 200 adults). At the lower rate of marine mortality (0.84), none of the simulated populations went extinct. At a mortality rate of 0.94, most populations slowly increase over time. Some of the populations starting at 30 adults go extinct, although most populations recover. None of the simulated populations went extinct from the 250 adult starting population size. At a mortality rate of 0.99, all populations went extinct within 25 years. As expected, recovery times are much more rapid from a larger starting population size.

To evaluate whether population persistence was sensitive to the amount of habitat available, we repeated the above analysis at different amounts of habitat from 1 to 3,500 habitat units. The mean annual mortality rate of immature salmon at sea was assumed to be 0.947 for these analyses. Under the simulated conditions, the populations are deterministically extinct and all simulated populations are gone within a 50 year time horizon (Figure 3.15). However, the time to extinction does change with the amount of habitat available for the population. These changes are greatest for smaller watersheds (less than 500 habitat units).

The above analyses suggest that population persistence in the long term is not very sensitive to habitat quantity above 500 habitat units. We examined the sensitivity of this conclusion to the parameter values used in the simulations by examining the interactions between the parameter values and habitat quantity. The results of these analyses are presented in contour plots in Figures 3.16 to 3.21.

Relative to habitat amount, the mortality rate of immature salmon at sea has a much greater effect on population persistence than habitat quantity except at low amounts of habitat (Figure 3.16). Large decreases in the amount of habitat had little effect on the probability of population persistence until habitat amount reached approximately 500 units, where further decreases had a large impact on population persistence. Conditional on the other model parameters, a sharp band exists for mortality rates in the range of 0.92 to 0.94 above which no populations were persistent and below which all populations were persistent except at freshwater habitat amounts below roughly 500 units.

Similar patterns were observed for both the egg mortality rate (Figure 3.17) and the mortality rates of age-1 and older parr (Figure 3.18). For each of these parameters a sharp band existed with a few percentage points separating extinction and persistence. Interactions with habitat amount occurred only at low habitat amounts. Note that the effect of these parameters on persistence does not pertain to recovery to historic

population sizes. In the case of the egg mortality rate, the equilibrium population size remains small (as shown in Section 3.4.1). This is to say that although persistence probability can be increased by increasing egg survival, recovery to population sizes observed in the 1970's cannot be achieved by only changing this parameter. The scenario is slightly different for the parr mortality rate, assumed here to occur after density dependence. Given this assumption, equilibrium population size will increase as the parr survival rate increases, but not to levels that reflect historic abundance without a change in survival at sea.

Our analyses also shows that the adult (post-spawning) annual mortality rate (Figure 3.19) can affect population persistence and that it interacts with habitat amount in ways that are similar to parr and egg mortality. At the values used for the other model parameters, adult mortality rates need to be less than 10% annually to ensure a 90% probability of persistence for 250 years. Our estimate of the adult annual mortality rate for the pre-1990 time period (0.495) substantially exceeds this value. Although not shown here, our analyses indicate that this result is quite sensitive to the assumed mortality rate for immature fish at sea. At higher smolt to adult return rates, repeat spawning (the outcome of decreased adult mortality) is less important for ensuring population persistence. Here again, historic population sizes cannot be achieved only by changing this parameter, at least within reasonable limits.

Increasing the probability of smoltification at age-2 tended to increase population persistence in the short term, but even if all salmon smoltified at age-2, the populations are deterministically extinct (Figure 3.20). A similar pattern exists for the probability of maturing after one winter at sea (Figure 3.21), because, given the other parameter values, the equilibrium population size was zero irrespective of the sea age at maturity. All simulated populations were extinct in 50 years. Changing the proportion of fish maturing after one winter at sea only slightly changed the time horizons to extinction.

The slope at the origin (alpha) of the spawner-recruit model used to describe the density dependent survival for parr between age-0 and age-1 also affected time horizons to extinction, although even at a value of one, all populations were extinction within 50 years (Figure 3.22).

4.0 Discussion

4.1 Summary and evaluation of the critical habitat assessment

Overall, the analyses presented herein suggest that a freshwater critical habitat designation for iBoF salmon would have little effect on population persistence under present marine survival conditions. Results from both the deterministic and stochastic models show that large changes in habitat amount have little effect on lifetime reproductive rate and population persistence under currently high rates of marine mortality. However, the analyses also show that if marine survival increases, population recovery rates are sensitive to both the quantity and quality of freshwater habitat and hence critical habitat designations may assist with population recovery under these conditions. The limitations and caveats of the analyses presented form much of the discussion that follows.

We are not claiming that no freshwater habitat issues exist within iBoF rivers. Habitat loss in the iBoF may have reduced regional abundance historically (Perley 1852, Watt 1989), but populations recovered as fish passage and water quality issues were resolved on many of these rivers. Barriers to fish passage, habitat loss due to a variety of factors, and water quality issues are present in some inner Bay of Fundy rivers, although such issues have not been identified on many rivers. At present, no strong link between these factors and marine survival has been discovered for iBoF rivers. The analyses presented herein indicate that population viability and specifically recovery to conservation limits cannot realistically be achieved by increasing the quantity or quality of freshwater habitat under current marine survival conditions.

These conclusions may contrast with studies of many endangered populations where the principal threat is habitat loss. Here, the key issue is the role and timing of density dependent (compensatory) processes in regulating population size. Small populations which are near their carrying capacity, but do not have much habitat, will be the most responsive to changes in habitat amount. Under this scenario, any increase in habitat should decrease density dependent interactions and promote population growth. When the cause for the decline is density independent (not compensatory), changing carrying capacity (and thereby density-dependent interactions) would not be expected to markedly change population viability. Our analyses indicate this is the case for iBoF salmon.

An alternate density dependent scenario occurs when survival rates increase with increasing abundance, a phenomenon known as depensation, an issue that remains a fundamental uncertainty in fisheries biology. Myers et al. (1995b) did not find evidence of depensation in 125 of 128 spawner-recruit time series they examined. Liermann and Hilborn (1997) conducted a similar analysis with a different depensatory model and concluded that depensation may be more common than suggested by Myers et al. (1995b). Populations that undergo large declines often do not rapidly recover (Hutchings 2000, Hutchings 2001), possibly indicating that depensatory population dynamics may be quite common. If so, the use of purely compensatory models, such as was used herein, would be inappropriate. Two things would be required if depensation is limiting the

recovery of iBoF salmon: population sizes would have to be increased to a size where compensation is again occurring (which could potentially be accomplished via the LGB program) and enough habitat would have to be available to maintain populations at levels above the point where depensation begins to occur.

Our analyses indicate that stochastic variability may place populations at risk when the amount of habitat drops below roughly 500 units (this value is sensitive to the assumed variability for the life history parameters). Of the 22 iBoF rivers for which habitat measurements are available (Section 2.5.3), four rivers have less than 1,000 habitat units in the gradient categories greater than 0.12 % and less than 5 % (Amiro et al. 2003: Table 2) and 12 have more than 3,000 habitat units.

The LGB program acts, to some extent, as a litmus test for freshwater habitat. Gibson et al (2004) provide summaries of the survival of LGB progeny as well as current return rates for adults. For example, the release of 34,000 age-0 parr in the Big Salmon River in 2002 resulted in the production of about 5,000 age-1 smolt in 2003. More of these fish are expected to smoltify in 2004 and 2005. Similarly, about 35% of the not-adipose-clipped smolt emigrating from Big Salmon River are thought to be LGB progeny released as fry, based on genetic comparisons with the parental crosses used to produce the fry. Present return rates are lower than predicted by the model. Based on the 2003 spawning run in the Gaspereau River, return rates of LGB smolt as 1SW salmon was 0.02 %, and of wild smolt returning as 1SW salmon was 0.83 %. These values support the modeling conclusions that the freshwater habitat can still support salmon populations and indicate that the downturn in marine survival is ongoing and perhaps worsening.

4.2 Limitations of data, model and survival/recovery goals

As is the case with any modeling exercise, our results are largely contingent on the model structure and assumptions. Consequently, several caveats must be attached to our conclusions. These caveats, as well as their implications for a potential critical habitat designation and recovery planning are discussed in this section.

In the model presented, we modeled freshwater habitat quality using only survival from age-0 to age-1, whereas freshwater habitat quality would also be expected to effect the survival of eggs and parr older than age-1 (Gibson 1993). This simplifying assumption would affect the estimates of population viability at low size, but does not effect the conclusion that populations cannot be restored to historic levels without a change in marine survival. This is shown through comparison of the equilibrium population sizes in Figure 3.8. No matter how steep the slope at the origin of the spawner-recruit function (here in units of smolt/egg), the equilibrium population size remain much lower than the size in the 1960's and 1970's.

We assumed that the survival and stage transition probabilities were constant through time with one single abrupt change somewhere in the series. This step function is only a first approximation of the timing and magnitude of changes in the life history parameters, whereas the true patterns are almost certainly more variable. However, as pointed out above, comparison of the model results with current data indicates that the true extent of

the decrease in marine survival is probably underestimated when the step function is used. As a result, population viability is overestimated and extinction is even more imminent than suggested herein, but the conclusion that a freshwater critical habitat designation would not be beneficial would not be altered if marine survival is overestimated by the model.

We did not include temporal autocorrelation when introducing random variability to the life history parameters in the PVA. Many populations cycle due to density dependent processes with time lags (Turchin 2003) and/or environmental forcing (McCann et al. 2003) and cycling is common in fish populations (Kendall et al. 1998). In the analysis of 694 time series of 220 species, Kendall et al. (1998) found that Atlantic and North Sea fish populations were more likely to cycle than Pacific populations. Furthermore, they found that cycle amplitude declined with latitude in salmonids. These results suggest that Atlantic salmon populations in the southern part of their range are prone to cycling. If so, our results indicate that the iBoF salmon may be in a trough of a cycle. Interactions between density dependent processes and the environment can affect the period and amplitude of population cycles (Myers et al. 1998, McCann et al. 2003). The response of a population to environmental variation (e. g. cycles in ocean temperature) is mediated by the type of density dependence (compensatory or over-compensatory). Populations with compensatory density, as modeled in this study, more closely track changes in environmental conditions than populations with over-compensatory density dependence. McCann et al. (2003) warn against assuming a population is viable when occasional rebounding occurs. They tentatively suggest that extinction probability increases when the frequency of cycles matches the age structure of the population.

Not accounting for temporal autocorrelation could have at least three effects on our conclusions. First, it affects our estimate of the timing of population collapse if populations appeared viable at high marine survival rates when they were not viable on longer time scales. Second, it affects our estimates of minimum viable population size (recovery targets) if populations need to be large enough to survive through cycle troughs. Third, more habitat would be required to maintain these larger populations and could be critical for population persistence. However, at this time, populations are at very low levels and are presently not viable. A freshwater critical habitat designation would not alter this basic result although it may be necessary for long-term persistence if populations show signs of recovery.

In this study, we modeled population dynamics for an entire river and did not include spatial variability within a river or straying between rivers. Metapopulation structure can increase regional persistence, particularly when dispersal 'rescues' a local population from extinction (Hanski 1998). Recent work on salmon populations indicate that even low straying rates can prolong regional persistence (Hill et al. 2002, Legault in prep). Maintaining links between populations by reducing incidental capture in other fisheries could improve the probability of persistence. Metapopulation theory suggests that the regional persistence of iBoF salmon is not only dependent on a few productive rivers, but also on straying rates and the number of occupied rivers. Even unoccupied rivers (and currently there are many) can also increase the probability of regional persistence if they

remain open to re-colonization. Here, the exclusion of meta-population structure from the model would lead to an underestimation of population persistence times. However, given that all iBoF salmon populations are at extremely low levels, the potential for a rescue effect from within the inner Bay is small. At present, a freshwater critical habitat designation would not alter this conclusion, but could potentially increase population recovery if marine survival increases.

One principal concern of population viability analysis is the incorporation of uncertainty (Ludwig 1999, Ellner et al. 2002). With the available data, we had difficulty obtaining parameter estimates, let alone estimates of their variances. We selected the variance for the spawner-recruit relationship based on the literature (Myers et al. 1995a), and set the variances for all other life history parameters at a constant rate. Our stochastic analysis then incorporates this variability, and carries it forward in our evaluation of the role of a critical habitat designation on population persistence and recovery. If we overestimated the parameter variances we would also overestimate the population size (and hence amount of habitat) required to offset demographic stochasticity. Here again, the equilibrium analyses (that do not include variability) indicate that populations are not viable at present survival rates and better estimates of process variability will not alter this fundamental conclusion.

It could be argued that a critical habitat designation would be beneficial for the "in-river" component of the LGB program (Amiro et al. 2003). Here, salmon of various ages are released into the rivers to provide exposure to the natural environment to allow natural selection to occur. A portion of these fish are then recaptured and brought back into the captive component of the program and mated according to a strategy designed to minimize inbreeding depression. Consequently, some habitat is required to support the "in-river" component of the LGB, although it is uncertain whether this habitat has to be tied to a specific location.

The majority of this document is focused on the freshwater environment, although critical habitat designation of the marine environment should also be considered (Amiro et al. 2003). The focus on the freshwater habitat in this document is the result of data being available on the distribution and abundance of salmon entering, inhabiting and leaving fresh water. Much less information is available on the distribution of iBoF salmon in the marine environment, and the timing and location of mortality at sea is unknown. We assumed that survival at sea was density independent in the models used herein, an assumption that precludes the possibility of affecting recovery by changing habitat amount. However, Amiro et al. (2003) reported that tag recoveries for iBoF salmon are roughly correlated with sea surface temperature. If sea surface temperature causes iBoF salmon to aggregate at predictable locations and times, these areas could potentially be deemed critical. At present we simply do not have the data to evaluate this possibility.

Recovery targets have not been established for iBoF rivers, and currently there is no method for identifying when recovery has occurred. Selection of recovery targets may necessitate combining approaches based on habitat amount and minimum effective population size. A major barrier to combining these methods is the lack of accurate N_e

/N_{census} ratios for Atlantic salmon. Of the two methods presented herein, the conservation limits used for fishery management are the lower targets for most iBoF rivers (assuming populations in individual rivers are closed). If the conservation limits were accepted as the recovery targets, then all habitat in these rivers would be deemed critical for recovery as these conservation limits are based on the amount of habitat in the rivers. At present, iBoF salmon populations are not recovering, extirpations have occurred in many rivers, and research effort would be better focused on how to rebuild the populations rather than on further refinement of a recovery target that is unlikely to be achieved in the near future.

4.3 Management advice, given current state of knowledge

The analysis presented here indicates that iBoF salmon have an equilibrium population size of zero and, in the absence of human intervention or a change in marine survival, will go extinct in the not too distant future. This conclusion is not sensitive to freshwater habitat quantity and as a result, protecting against habitat loss via a freshwater critical habitat designation will not increase population persistence. All results indicate that large changes in habitat quantity and quality have little effect on lifetime reproductive rate and population persistence under currently high rates of marine mortality. If marine survival increases, population recovery rates are sensitive to both the quantity and quality of freshwater habitat and hence critical habitat designations may assist with population recovery. Salmon habitat is presently protected under the Fisheries Act, and some parts of iBoF rivers presently have higher levels of protection: 77% of the Upper Salmon River and 58% of Pointe Wolf River are within federally protected land (Fundy National Park), although these represent only a small fraction of the total area historically occupied by iBoF salmon. If possible under SARA, deferring a freshwater critical habitat designation until populations show signs of recovery would avoid duplication of protection of habitat where salmon are not present and would also avoid the situation where habitat in rivers where salmon no longer exist (some iBoF rivers) receive a higher level of protection than habitat in rivers where salmon still exist (outside the inner Bay). The alternative, based on the adoption of the conservation limits as recovery targets, is to designate all freshwater habitat around the iBoF as critical to maintain the potential for recovery. This approach seems more consistent with the SARA but results in the situation just described. The provision to protect critical habitat could then be via the existing legislation in the form of the Fisheries Act.

Both the data and analyses presented indicate that extinction of iBoF is imminent in the absence of human intervention. To date, the most successful intervention has been the LGB program, and it is possible that iBoF salmon would presently be extinct had this program not been initiated. The program has been successful in increasing the numbers of salmon held in captivity, as well as the numbers of juvenile salmon in some rivers (see Figure 2.2). While the program appears successful in halting or slowing the decline of iBoF salmon, and also appears necessary to maintain populations until the causes of the high marine mortality are identified, it has been recommended that the use of "conservation hatcheries" should be temporary to avoid the dysgenic effects of domestication (Myers et al. 2004). So while the LGB program appears to be necessary to maintain populations until marine mortality decreases, it alone is unlikely to be a

sufficient measure to recover iBoF salmon and may not be a long-term solution to ensure their persistence. Identification and mitigation of the causes of the high marine mortality is required to affect recovery of these populations. However, as illustrated with the recovery trajectories (Figures 3.13 and 3.14), recovery is more rapid from a larger starting population size than a smaller size. In the event that marine survival increases, an added benefit of the LGB program is the potential to rapidly increase population sizes in the early recovery stages, thereby substantially lowering recovery times.

4.4 Evaluation of the draft critical habitat evaluation guidelines

When evaluating the efficacy of a critical habitat designation for survival or recovery of an endangered species, a comprehensive understanding of the reasons for the decline is required. For species with a limited geographic range and whose abundance is tracking a declining carrying capacity as a result of habitat loss, a critical habitat designation as part of a recovery strategy is intuitively appealing. For species with wide geographic ranges, that are migratory, and whose abundances are declining for some reason other than habitat loss, the role of critical habitat designation is less clear. Our data and analyses indicate that freshwater habitat around the inner Bay is abundant and sufficient to support juvenile Atlantic salmon. However, populations are presently not viable, and based on these analyses, viability does not change with further protection through a critical habitat designation. Habitat is presently protected under the Fisheries Act. It's likely that many fish populations will follow this scenario, and the document would benefit greatly if instruction and examples were provided for the designation of critical habitat when habitat is not the limiting factor.

One reason that iBoF salmon were included as a case study was because they were considered "data-rich". However, given the data for this population, we had sufficient difficulty providing estimates for the life history parameters, let alone estimates of their variances. It is these variances that will determine population viability (if determined using population simulations) and hence the amount of habitat required for persistence. One suggestion has been to use parameter values from other, similar populations if values are not available, but this practice could lead to overly optimistic scenarios for recovery if the parameter values are taken from populations that are presently viable. In the iBoF salmon example presented, the population is simply not viable, a conclusion that is not sensitive to parameter variability. However, in cases where the equilibrium population size is greater than zero, estimation of process variability will be key for determining critical habitat amounts, and the guidance document could benefit from suggestions on approaches for obtaining parameter estimates and associated variance rather than only on their use once the estimates are obtained.

The equilibrium analyses presented herein provide an alternative to PVA's for assessing recovery options. These types of models are relatively well developed in the fisheries literature and typical applications include estimating biological reference points for fisheries management. Changes in equilibrium population size (an attractor, based on birth rates, death rates, growth rates and carrying capacity, towards which the population size is expected to move) from recovery actions can be used to evaluate recovery strategies. The models are appealing because they are less data intensive than PVA's, but

are not suitable for evaluating risk from demographic stochasticity or autocorrelation in life history processes. A key advantage is their application for assessing viability via equilibrium population size. If viability is assessed only via persistence determined by a PVA, populations that are deterministically extinct (have equilibrium population size of zero) could persist through the time horizon used to assess persistence. An extreme example would be a population with an equilibrium size of zero, which is supplemented through captive-rearing and increased to a relatively large size, would have a longer time to extinction than a population with identical life history characteristics that has not received supplementation. The equilibrium calculations also highlight that population viability is not a function simply of population size. Recovery targets should therefore include statements about sustainability which could be evaluated using these types of models. This category of model could be included as an option in the guidance document.

4.5 Data gaps, science needs and recommended next steps

Mortality rates of immature iBoF salmon at sea are extremely high, and contrast sharply with the rates currently observed in many European populations and elsewhere in Canada (Amiro 2003b, Chaput et al. 2003, Ó Maoiléidigh et al. 2003), with the possible exception of some outer Bay of Fundy Rivers (Jones et al. 2004). Identification and mitigation of the cause(s) of the current high rates of marine mortality are critical if iBoF salmon are to be recovered. Possible explanations include natural cycles (e.g. the North Atlantic Oscillation), predation at sea, oceanic regime (physical or biological) shifts, interactions with aquaculture and genetic effects. Some support exists for each of these hypotheses, although none are unequivocal, and the reasons for the declines in survival of iBoF salmon may differ from the reasons for declines in other populations in Atlantic Canada.

Ocean temperature cycles known as the North Atlantic Oscillation correlate with historical landings, and it has been suggested that long-term positive forcing (global warming) may be the cause of current declines (Friedland et al. 2003). The largest increases in sea surface temperature around the globe have occurred in the North Atlantic, which has been related to a decrease in primary productivity (Gregg et al. 2003). These observations suggest that the recent declines in Canadian salmon populations could be due to global warming. These mechanisms are perhaps more accepted among scientist working on Pacific salmon. The mortality of Pacific salmon at sea has been linked to the changes in ocean productivity caused by the El Nino-Southern Oscillation (Francis and Hare 1994, Beamish et al. 1999). Levin et al. (2001) found that the marine survival of wild chinook salmon was negatively correlated with the number of hatchery fish released when ocean conditions were poor, suggesting that food limitation occurs. Their index of productivity probably best represents near-shore conditions, which would further suggest that food limitation may occur in the first few months after entering the sea.

Increases in aquaculture, predators, and disease have also been implicated as causes for increased morality rates (Johnsen and Jensen 1994, Baum 1997). One important concern is the transfer of disease from aquaculture fish to wild populations. Heavy infestations of

salmon lice (*Lepeophtheirus salmonis)* can cause an increase in the sea mortality of post-smolts (Grimnes and Jakobsen 1996, Finstad et al. 2000). Disease can rapidly spread among populations, potentially having negative impacts on abundance. In Norway the disease furunculosis spread to 52 rivers in three years (Johnsen and Jensen 1994).

This study has not focused on the role of genetics in population viability, however, we do wish to acknowledge its importance. Several studies of European populations indicate that interactions between escaped farm salmon can have detrimental effects. Farmed salmon may compete for territories and food, and displace wild salmon (Einum and Fleming 1997, McGinnity 1997). Fleming et al. (2000) found that the lifetime reproductive success of farm salmon was 16% of wild. Interbreeding with wild salmon resulted in a 30% decrease in the productivity of the native population.

Almost nothing is known about the predator-prey dynamics of salmon at sea. Most prey species (e. g. sandeels, *Ammodytes* sp.) are not well covered in current fish surveys, and consequently it is difficult to asses the influence of prey abundance on marine survival. Salmon post-smolts have a broad diet, and it is unlikely that they would be sensitive to fluctuations in a single species (Hislop and Shelton 1993). However, it appears that 'forage fish' as a group have increased in recent years (Choi et al. 2004), suggesting that older piscivorous post-smolts may not currently be food limited. Since many species eat salmon at sea, it is difficult to estimate the impact of predation on marine survival. One study of chinook salmon (*Oncorhynchus tshawytscha*) found that even low levels of mortality caused by striped bass (*Morone saxatilis*) can increase the probability of extinction (Lindley and Mohr 2003). The Bay of Fundy has unique hydrological characteristics which may affect survival at sea, and some information indicates that iBoF salmon may not typically migrate far beyond the Bay of Fundy (Jessop 1976, Amiro et al. 2003). Linking mortality to specific places and times will likely be an important step in understanding the principal causes of marine mortality (Lacroix and McCurdy 1996).

From the perspective of designating critical habitat, the data and analyses presented herein are sufficient for decisions about freshwater designations if the conservation limits are adopted as recovery targets, but further information about their distribution at sea is required for a designation in the marine environment. Sonic tagging and surface trawling are two methods that could be used to collect information about their distribution. Further refinement of recovery targets based on minimum effective population sizes would require information about straying rates that would have to be inferred from populations outside the inner Bay. A thorough understanding of the timing and nature of density dependence is required to build population models, including knowledge of inter-cohort interactions, whether processes are compensatory, depensatory and/or over-compensatory, the presence of time lags and how density dependence influences population distribution. Further research into these areas would certainly improve our knowledge of salmon population dynamics, but we do not anticipate it would change the conclusions drawn here about the efficacy of a critical habitat listing.

From the perspective of recovering iBoF salmon, the key question remains of why survival at sea is as low as it is. One potential method of addressing this question, based

on the idea that other salmon populations are in jeopardy as well, would be a meta-analysis of population trends in eastern North America. The characterization of the spatial and temporal pattern in declines of salmon populations would provide a baseline against which potential causes of declines (e.g. predator abundance, oceanic conditions, etc.) could be correlated. In order for correlates to be found, estimates of marine survival are required, and monitoring of smolt migration and adult returns, such as is presently occurring on the Big Salmon River, provide the basis for its estimation.

Further elucidation of the timing and location of mortality at sea may well require field experiments. Tagging studies that can provide information on the timing and location of mortality at sea would provide the most direct determination of the sources of mortality for iBoF salmon.

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7.0 Tables

Table 2.1. Summary statistics for the Atlantic salmon recreational catch (number caught) and fishing effort (rod days) for 17 inner Bay of Fundy rivers, from 1960 to 1990 (1954 to 1990 for the Big Salmon River). "N" is the number of years for which data are available. Data for Nova Scotia rivers are the number of fish that were caught and for New Brunswick rivers are the number of fish harvested (from Gibson et al. 2003b).

		Catch					Effort				
River	N	mean	std. dev.	Min.	max.	median	mean	std. dev.	min.	max.	median
Big Salmon, NB	37	373.1	321.6	6	1,321	281	4,860.1	7,645.8	320	41,317	2,358
Black River, NB	19	29.2	41.7	0	162	12	566.6	728.6	40	2,625	244
Cornwallis, NS	23	4.2	7.1	0	34	2	92.2	59.8	21	240	90
Debert, NS	26	68.9	57.0	2	230	62	263.8	185.7	15	660	241
Economy, NS	25	63.0	54.0	4	194	58	213.2	167.5	15	645	200
Folly, NS	25	96.0	90.9	4	356	73	321.8	205.9	15	810	330
Gaspereau, NS	31	27.3	22.8	3	92	23	369.0	142.2	88	665	360
Great Village, NS	20	7.9	10.6	0	42	4	29.8	28.6	4	110	16
Maccan, NS	26	105.2	68.1	6	291	94	513.1	327.7	20	1,272	412
North (Truro), NS	25	57.3	51.6	2	153	40	194.2	154.3	10	497	164
Petitcodiac, NB	21	48.8	73.4	0	304	20	251.9	229.5	50	1,020	180
Portapique, NS	26	36.2	32.6	3	120	20	128.4	110.2	13	390	89.5
Salmon (Truro), NS	19	70.5	56.6	4	192	54	298.4	240.4	47	1,006	210
Shubenacadie, NS	27	94.7	84.9	0	298	72	607.6	528.8	4	1,890	464
Stewiacke, NS	31	575.3	491.9	0	1,980	474	2,983.5	2,227.5	35	9,267	2,347
Upper Salmon, NB	24	76.1	62.3	3	211	66	288.8	133.4	35	613	311

Table 2.2. Summary of the Atlantic salmon counts at the White Rock fish ladder on the Gaspereau River, NS, from 1997 to 2003 (from Gibson et al. 2004).

			Year						
	Origin	Size	1997	1998	1999	2000	2001	2002	2003
Released into river:	Wild	Large	5	6	11	3	6	0	0
		Small	30	9	1	7	7	0	0
	Hatchery	Large	2	10	13	4	10	0	0
		Small	22	42	0	30	5	0	0
Retained for broodstock:	Wild	Large	7	3	14	4	14	0	2
		Small	23	7	2	14	6	8	2
	Hatchery	Large	5	2	0	9	3	4	0
		Small	8	20	0	5	6	2	3
Total count:		Large	19	21	38	20	33	4	2
		Small	83	78	3	56	24	10	5
Total count all sizes:			102	99	41	76	57	14	7
%		counted	74	56	30	16	24	8	5
Conservation		escapement	43	42	15	9	18	0	0

Table 2.3. Life history table. For North American salmon of wild origin only.

Trait	Stage	River, Region	Years of Data	Mean	SE	Min	Max	Reference
Fecundity	adult, small	Big Salmon, NB		3233		2217	6602	Amiro, Farmer, and Goff (unpublished data)
	adult, large	Big Salmon, NB		5541		2841	13808	Amiro, Farmer, and Goff (unpublished data)
Survival to next stage (%)	egg to fry	Catamaran Brook, NB	6	30.67		9.20	61.0	Cunjak et al. 1998
	egg to fry	Pollett, NB		17.60		1.70	8.00	Elson 1957
	egg to fry	Morell, PEI	1			0	56	Cunjak et al. 2002
	egg to fry	Machias, Maine		25.00		15.00	35.00	Jordan and Beland 1981
	fry to parr-0	Cove Brook, Maine	2	10.15		8.9	11.4	Meister 1962
	egg to parr-1	Pollett, NB	8	6.11		2.8	16.3	Elson 1975, Symons 1979
	parr-0 to parr-1	Catamaran Brook, NB	6	34.17		15.00	75.00	Cunjak et al. 1998
		Cove Brook, Maine	2	50.25		41.10	59.40	Meister 1962

Table 2.3. Life history table. For North American salmon of wild origin only *(continued)*.

Trait	Stage	River, Region	Years of Data	Mean	SE	Min	Max	Reference
	parr-1 to smolt	Catamaran Brook, NB	6	32.92		25.00	47.50	Cunjak et al. 1998
		Cove Brook, Maine	1	8.90				Meister 1962
		Pollett, NB	8	46.10		14.00	81.00	Elson 1975, Symons 1979
	precocious	Little Codroy, NL	4	27.25		12.00	41.00	Myers 1984
	immature	Little Codroy, NL	4	43.75		30.00	72.00	Myers 1984
Age of smoltification		Big Salmon, NB	13	2.50	0.00818	1	4	Jessop 1986, Ritter 1989, + current data
Years of immature at sea		Big Salmon, NB	13	1.10	0.00501	1	3	Jessop 1986, + current data
Age of reproduction		Big Salmon, NB	13	4.34	0.0180	3	9?	Jessop 1986, + current data
Pervious spawning history		Big Salmon, NB	13	0.735	0.0150	0	5	Jessop 1986, + current data
Sex ratio M:F	adult	Big Salmon, NB	13	0.69	0.1244	0.34	1.75	Jessop 1986, + current data

Table 3.1. Estimates of the ratio between effective and census population sizes (N_e / N_{census}) for different salmonids

Species	Mean (N_e / N_{census})	Range	Reference
Chinook salmon (*Oncorhynchus tshawytscha*)	0.63	0.21 – 2.23	Waples et al. (1993)
		0.013 – 0.367	Bartley et al. (1992), Hendrick et al. (1995)
		0.12 – 0.84	Hard (2000)
		0.43 – 1.19	Hendrick et al. (2000)
		0.5 – 0.6	Waples (2002)
		0.021 – 0.765	Shrimpton and Heath (2003)
Coho salmon (*Oncorhynchus kisutch*)	0.24	0.20 – 0.38	Simon et al. (1986)
Pink salmon (*Oncorhynchus gorbuscha*)		0.28 – 1.0	Geiger et al. (1997)
Steelhead trout / Rainbow trout (*Oncorhynchus mykiss*)	0.90		Bartley et al. (1992)
		0.1 – 0.3	Heath et al. (2001)
		0.47 – 0.96	Ardren and Kapuscinski (2003)
Bull trout (*Salvelinus confluentus*)		0.5 – 1.0	Rieman and Allendorf (2001)
Across taxa and studies		0.26 – 0.88	

Table 3.2. Tests for density dependence for two inner Bay of Fundy salmon populations. Fits of linear models (density-independent) are compared with the fits of Beverton-Holt models (density dependent). P-values were calculated using likelihood ratio tests.

River	Stock	Recruit	Model	α	R_0	σ	NLL	p-value
Stewiacke	age-0	age-1	L	1.020		0.607	45.35	
	age-0	age-1	B-H	0.851	7.37×10^{11}	0.607	45.35	>0.990
	age-1	age-2	L	0.302		0.352	19.97	
	age-1	age-2	B-H	0.350	18.4	0.324	18.64	0.103
	age-0	age-2	L	0.302		0.730	27.46	
	age-0	age-2	B-H	0.259	27.1	0.725	27.34	0.624
Big Salmon	adult	age-0	L	0.023		0.677	43.00	
	adult	age-0	B-H	0.029	61.3	0.594	41.56	0.090
	age-0	age-1	L	0.649		0.417	18.41	
	age-0	age-1	B-H	1.080	21.6	0.253	14.92	0.008
	age-1	age-2	L	0.205		0.613	8.16	
	age-1	age-2	B-H	0.170	1.21×10^{12}	0.613	8.16	>0.990
	age-0	age-2	L	0.137		0.684	11.66	
	age-0	age-2	B-H	0.108	6.33×10^{11}	0.684	11.66	>0.990

Table 3.3. Data sets used to estimate life history parameters for Atlantic salmon in the Big Salmon River, NB. Actual data are provided in Jessop (1975), Jessop (1986) Gibson et al. (2003b) and Gibson et al. (2004).

Data set	Years available
juvenile electrofishing	1968, 1970, 1971, 1972, 1973, 1982, 1989 to 2003
redd counts	1996 to 2002
streamside obs. and dive counts for adults	1988 to 2003
recreational fishing catch and effort	1951 to 1990 (1964 to 1990 used herein)
fence counts for adults	1964 to 1973
fence counts for smolts	1966 to 1971
mark recapture estimates for smolts	2001 to 2003
adult sex, age and previous spawning data	1964 to 1973, 2001 to 2003
smolt age data	1966 to 1972, 2001 to 2003

Table 3.4. The statistical model used to estimate abundance of salmon in the Big Salmon River, NB. The relational equations are used to link the life history model to the data collected for this population.

Type of Equation	Equation	No.
Relational:	$N_{t,small} = \sum_{s,c,a} N_{s,c,a,0}$ for $p = 0$; $N_{t,large} = \sum_{s,c,a,p} N_{s,c,a,p}$ for $p > 0$	1
	$C_{t,g} = N_{t,g}(1 - e^{-F_{t,g}})$	2
	$F_{t,g} = q_g f_t$	3
	$Fence_{t,g} = N_{t,g}$	4
	$Redd_t = q_{\text{redd}} \sum_{s,a,c,p} E_{t,s,a,c,p}$	5
	$Swim_t = q_{\text{swim}} \sum_{s,a,c,p} E_{t,s,a,c,p}$	6
		7
Log Likelihoods:	$\ell_{catch} = -n \ln \sigma_{catch} \sqrt{2\pi} - \sum_{t,g} C_{t,g}^{obs} - \frac{1}{2\sigma_{catch}^2} \sum_{t,g} (\ln C_{t,g}^{obs} - \ln C_{t,g})^2$	8
	$\ell_{fence} = -n \ln \sigma_{fence} \sqrt{2\pi} - \sum_{t,g} Fence_{t,g}^{obs} - \frac{1}{2\sigma_{fence}^2} \sum_{t,g} (\ln Fence_{t,g}^{obs} - \ln Fence_{t,g})^2$	9
	$\ell_{electrofishing} = -n \ln \sigma_{elect} \sqrt{2\pi} - \sum_{t,a} P_{t,a}^{obs} - \frac{1}{2\sigma_{elect}^2} \sum_{t,a} (\ln P_{t,a}^{obs} - \ln P_{t,a})^2$	10
	$\ell_{swim} = -n \ln \sigma_{swim} \sqrt{2\pi} - \sum_{t} Swim_t^{obs} - \frac{1}{2\sigma_{swim}^2} \sum_{t} (\ln Swim_t^{obs} - \ln Swim_t)^2$	11
	$\ell_{redd} = -n \ln \sigma_{redd} \sqrt{2\pi} - \sum_{t} Redd_t^{obs} - \frac{1}{2\sigma_{redd}^2} \sum_{t} (\ln Redd_t^{obs} - \ln Redd_t)^2$	12
	$\ell_{age}^{smolt} = \sum_{t} \log\left(\frac{n_{smolt,t}!}{(x_{smolt,t,1}!)(x_{smolt,t,2}!)\ldots(x_{smolt,t,r}!)} p_{smolt,t,1}^{x_{smolt,t,1}} \ldots\ldots p_{smolt,t,r}^{x_{smolt,t,r}} \right)$	13
	$\ell_{age}^{adult} = \sum_{t} \log\left(\frac{n_{adult,t}!}{(x_{adult,t,1}!)(x_{adult,t,2}!)\ldots(x_{adult,t,r}!)} p_{adult,t,1}^{x_{adult,t,1}} \ldots\ldots p_{adult,t,r}^{x_{adult,t,r}} \right)$	14
Objective Function:	$O.F.V. = -(\ell_{fence} + \ell_{catch} + \ell_{electrofishing} + \ell_{swim} + \ell_{redd} + \ell_{age}^{adult} + \ell_{age}^{smolt})$	15

Table 3.5. Parameter maximum likelihood estimates (MLE) obtained from three models fit to the Big Salmon River Atlantic salmon data. In the "base" model, estimated life history parameters are assumed to be constant through time. In the "freshwater" model, the estimated life history parameters for the freshwater component differ between the pre-1990 and 1990 and later time periods, while the parameters for the marine component are assumed constant through time. In the "marine" model, the estimated life history parameters for the marine component differ between the pre-1990 and 1990 and later time periods, while the parameters for the freshwater component are assumed constant through time. Standard errors (SE) are obtained using the delta method under the assumption of asymptotic normality.

	Model									
	Base		Freshwater				Marine			
			pre-1990		1990 and later		pre-1990		1990 and later	
	MLE	SE	MLE	SE	MLE	SE	MLE	SE	MLE	SE
Sampling coefficients:										
electrofishing q	2.79E+03	8.19E+02	2.27E+03	4.66E+02			2.99E+03	2.93E+02		
stream and dive count q	3.57E-01	5.97E-02	4.78E-01	7.55E-02			5.13E-01	8.51E-02		
redd count q	1.46E-01	5.76E-02	3.43E-01	1.31E-01			3.49E-01	1.38E-01		
fishing q (small salmon)	-9.61E+00	7.38E-02	-9.63E+00	7.59E-02			-9.60E+00	7.61E-02		
fishing q (large salmon)	-9.59E+00	9.18E-02	-9.58E+00	9.36E-02			-9.48E+00	9.51E-02		
Life history parameters:										
egg mortality	9.65E-01	1.07E-02	9.80E-01	4.09E-03	9.61E-01	8.98E-03	9.59E-01	3.15E-05		
Beverton-Holt α	5.00E-01	6.54E-02	5.15E-01	3.16E-02	9.09E-01	1.11E-01	6.29E-01	7.20E-02		
Beverton-Holt R_0	7.04E+02	1.42E+03	4.86E+01	2.09E+01	5.59E+02	6.74E+02	8.71E+01	3.12E+01		
parr mortality	6.23E-01	6.32E-02	2.35E-01	7.60E-02	8.53E-01	1.68E-02	6.13E-01	3.38E-02		
sea mortality (immature)	8.12E-01	4.38E-02	7.15E-01	4.45E-02			8.29E-01	2.56E-02	9.70E-01	1.42E-02
sea mortality (post-spawn)	5.02E-01	9.20E-03	5.00E-01	9.22E-03			4.95E-01	9.88E-03	6.43E-01	2.52E-02
prob. smolt age-2	2.90E-01	3.80E-02	4.41E-01	2.61E-02			2.96E-01	2.02E-02		
prob. smolt age-3	9.09E-01	1.51E-02	9.51E-01	6.09E-03			9.11E-01	9.63E-03		
prob. maturing 1SW	2.87E-01	8.31E-02	1.22E-01	2.38E-02			2.63E-01	5.32E-02	8.40E-01	3.86E-01
smolt sex ratio	2.77E-01	7.90E-03	2.77E-01	7.91E-03			2.78E-01	7.90E-03		
Population initialization:										
number of eggs (1959)	7.28E+06	2.19E+06	1.61E+07	3.60E+06			8.40E+06	1.89E+06		
number of eggs (1960)	4.62E+06	2.02E+06	1.78E+07	6.08E+06			5.63E+06	1.82E+06		
number of eggs (1961)	2.95E+06	7.21E+05	6.77E+06	1.58E+06			3.33E+06	6.30E+05		
number of eggs (1962)	4.13E+06	1.01E+06	4.40E+06	8.93E+05			4.65E+06	5.87E+05		
number of eggs (1963)	6.54E+06	2.59E+06	2.98E+06	7.70E+05			7.52E+06	1.07E+06		
number of eggs (1964)	1.03E+07	6.08E+05	9.95E+06	5.84E+05			1.00E+07	6.01E+05		
Objective function value:	3399.9		3210.5				3359.0			

Table 3.6. Constants used in PVA model.

	Name	Stage	Value
Life history parameter:			
	Fecundity	adult, 1SW	3232
		adult, 2SW	5540
	Max parr age		3
	Min age of smoltification		2
	Max age of smoltification		4
	Min number of years as immature at sea		1
	Max number of years as immature at sea		2
	Min age of first reproduction		3
	Max number of previous spawnings		5
	Max age		10

Table 3.7. Stock-recruitment relationships for Atlantic salmon in North American rivers. A Beverton-Holt relationship with lognormal error was assumed. Data are from the Myers stock-recruitment database (Myers et al. 1995a). See http://fish.dal.ca/~myers/welcome.html for more information.

Stock to Recruit	River, Region	Years of data	Alpha	R_0	Sigma
Eggs to smolt (age 3)	Bec-Scie, Quebec	6	0.0363	6680	0.206
Eggs to smolt (age 2.5)	Little Codroy, NL	7	107.0	12500	0.0896
Adults to adults (age 5)	Margaree, NS	34?	5.80	3700	0.491
Adults (large kelt) to parr (per $100m^2$)	Miramichi, NB	14	0.00416	570	0.320
Eggs to smolt (age 2.5)	Pollett, NB	9	46.1	16900	0.440
Adults (large salmon) to parr (per $100m^2$)	Restigouche, NB	12	0.00363	12.6	0.307
Eggs to adults (age 4)	Tobique, NB	10	4.23	25000	0.230
Eggs to smolt (age 3)	Trinite, PQ	9	0.314	76000	0.316
Adults to adults (age 6)	Western Arm Brook, NL	17	11.7	543	0.515
Adults to smolt (age 4)	Western Arm Brook, NL	16	84.2	23200	0.250
Min					0.09
Max					0.52
Mean					0.32

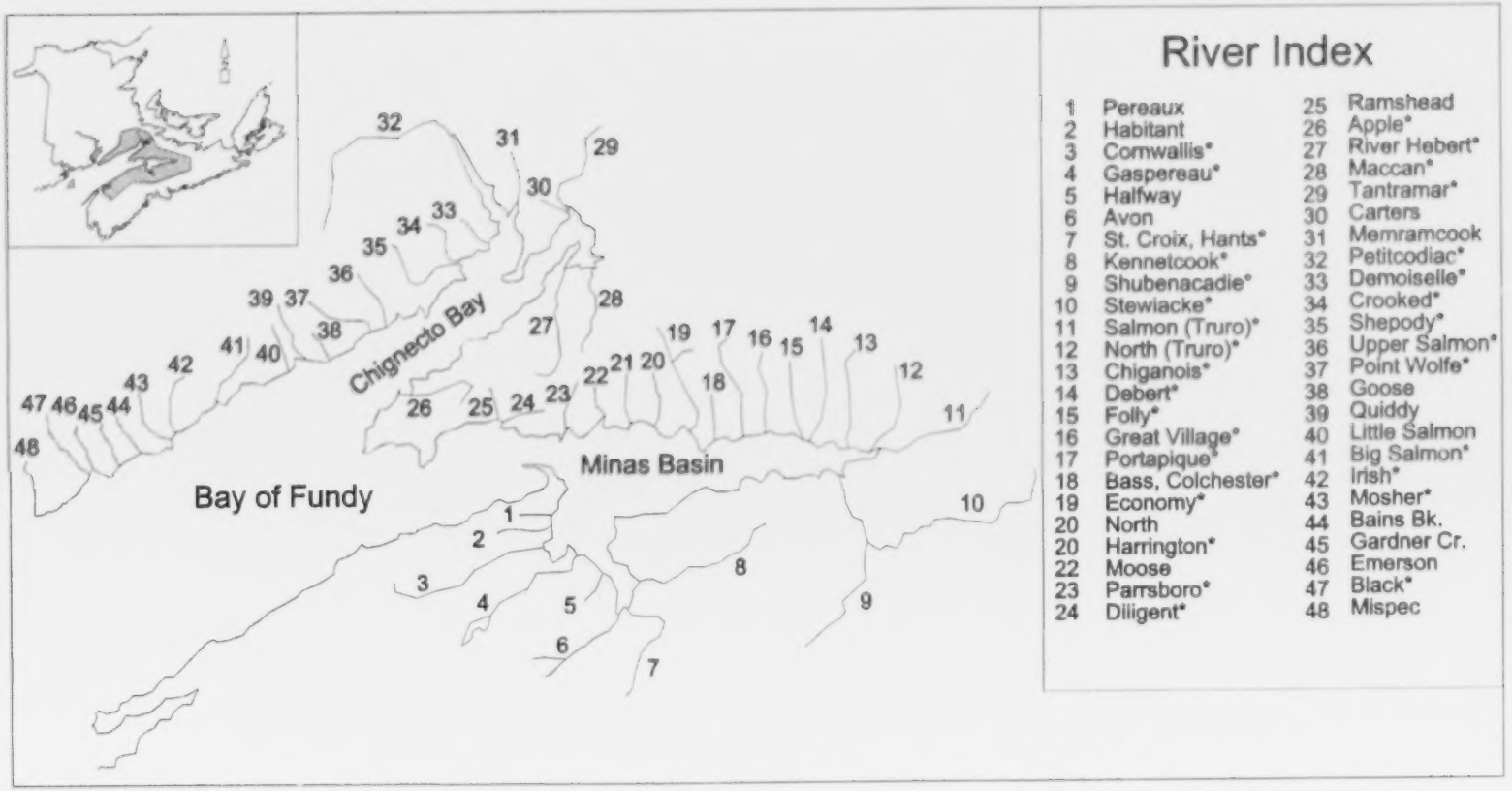

Figure 2.1. Map showing the approximate locations of inner Bay of Fundy rivers referred to in this report. Rivers in which a reported recreational catch, or electrofishing surveys confirmed the past presence of Atlantic salmon are marked with an asterisks (adapted from Amiro 2003).

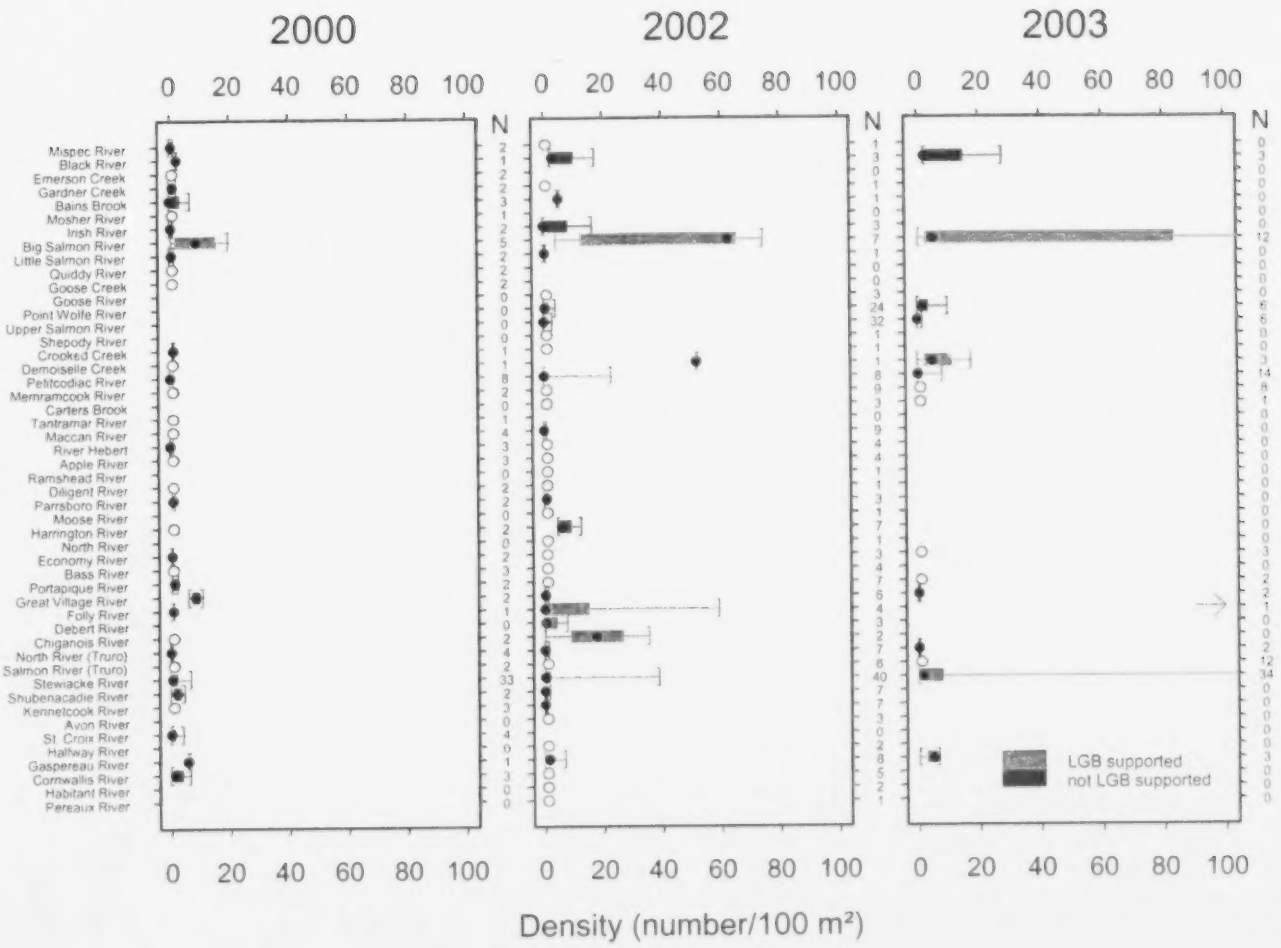

Figure 2.2. Box plots showing the density of Atlantic salmon in inner Bay of Fundy rivers based on electrofishing during 2000, 2002 and 2003. The dot shows the median density and the box shows the inter-quartile spread. The whiskers are drawn to the minimum and maximum. LGB (living gene bank) supported rivers are where juvenile Atlantic salmon had been released since 1996 and prior to electrofishing. Densities outside the range of the graph are marked with an arrow. O's mark rivers in which salmon were not captured. Rivers with blank spaces were not electrofished in those years.

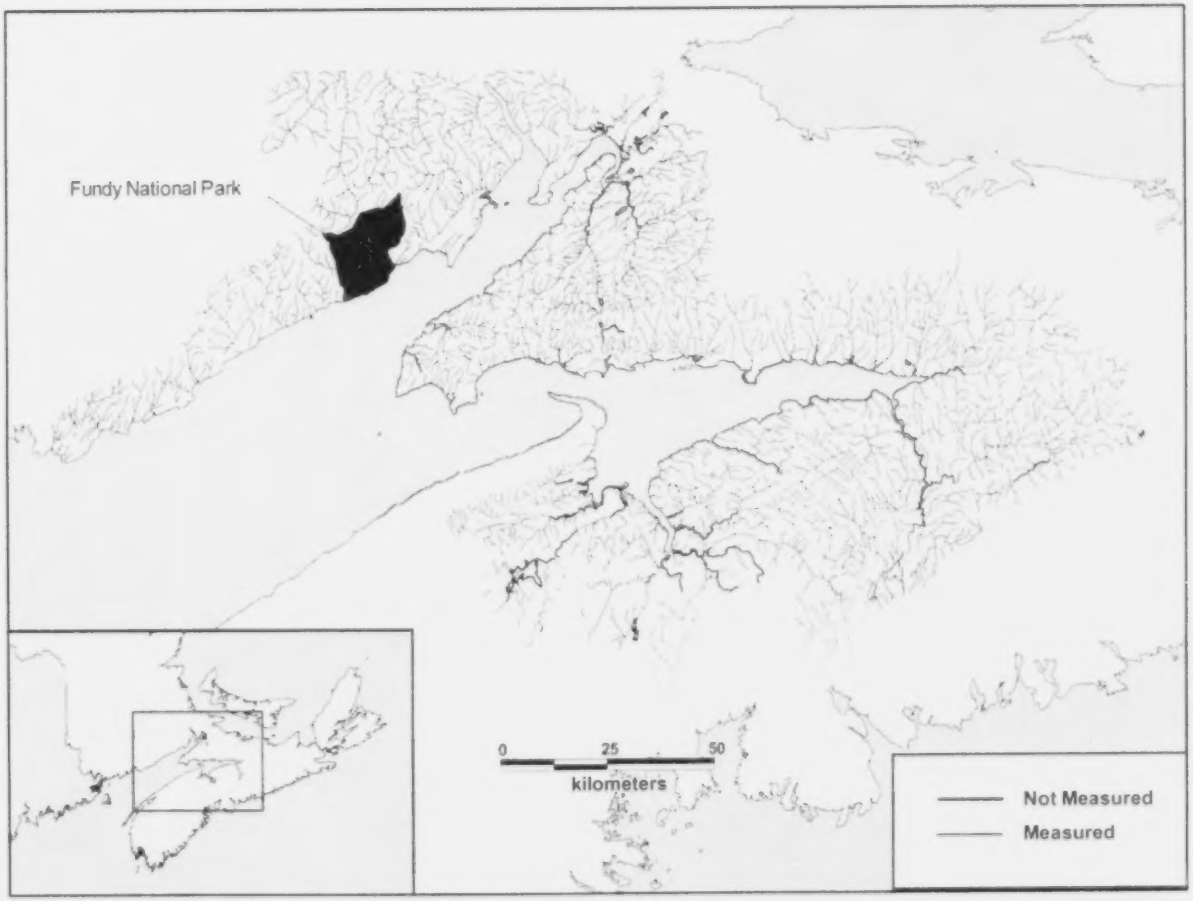

Figure 2.3. Map showing the extent of the habitat mapping for inner Bay of Fundy rivers (from orthophoto maps and aerial photographs). Not all of the Petitcodiac River watershed is shown.

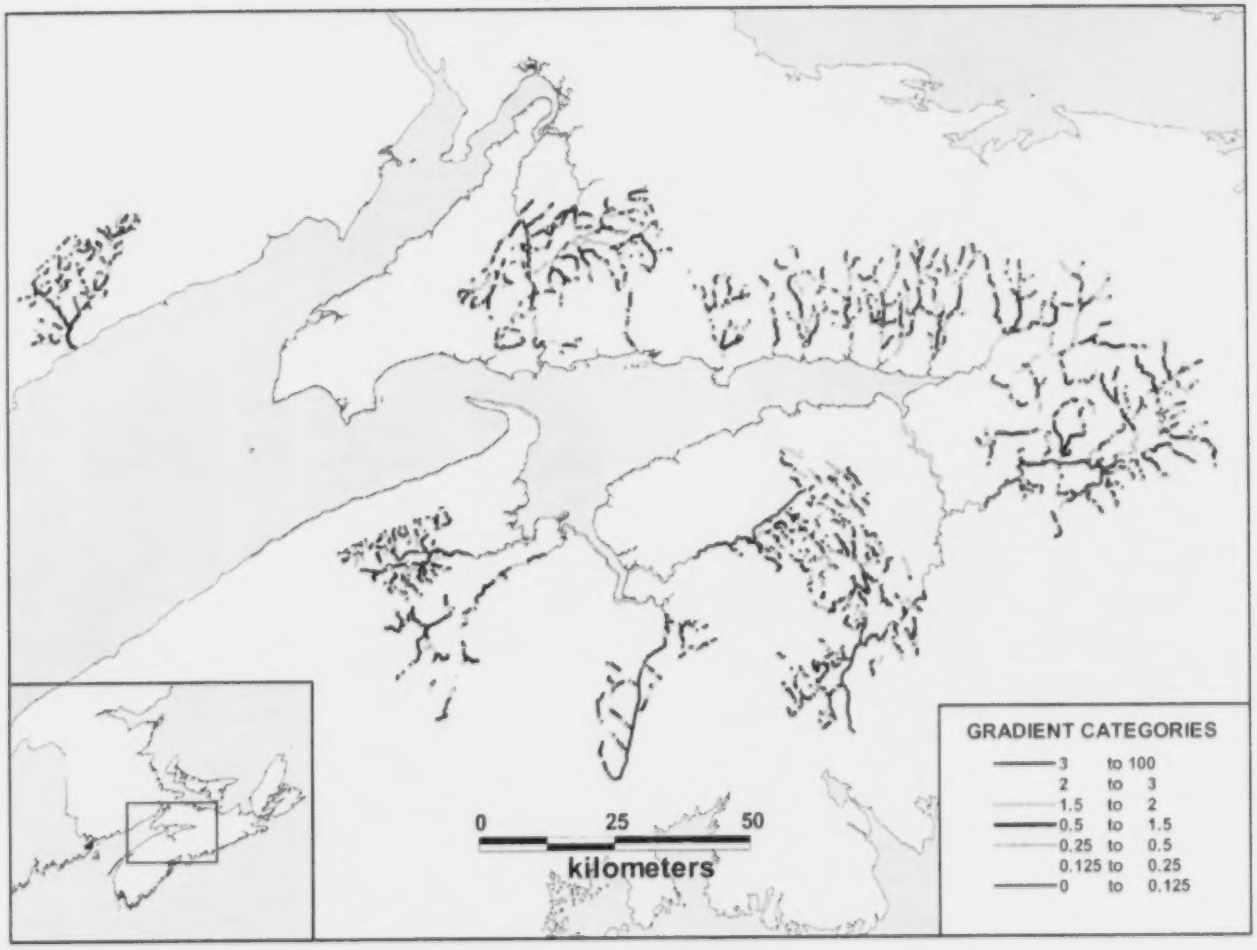

Figure 2.4. The gradient of 22 inner Bay of Fundy rivers. A gradient of 0.5 to 1.5 indicates optimal habitat (Amiro et al. 2003).

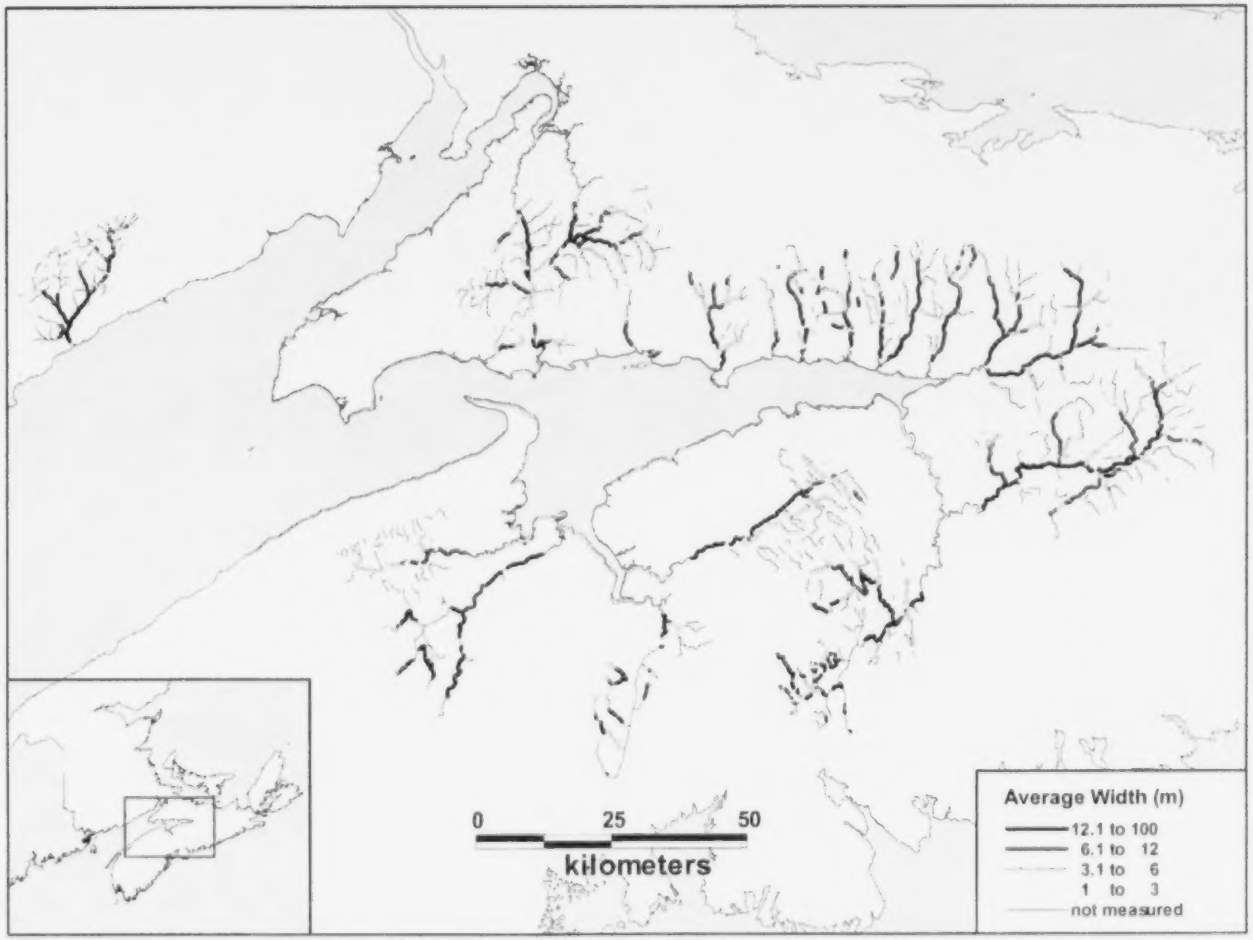

Figure 2.5. The width of 22 inner Bay of Fundy rivers. Gradient, length, and width can be combined to estimate productive capacity (Amiro et al. 2003).

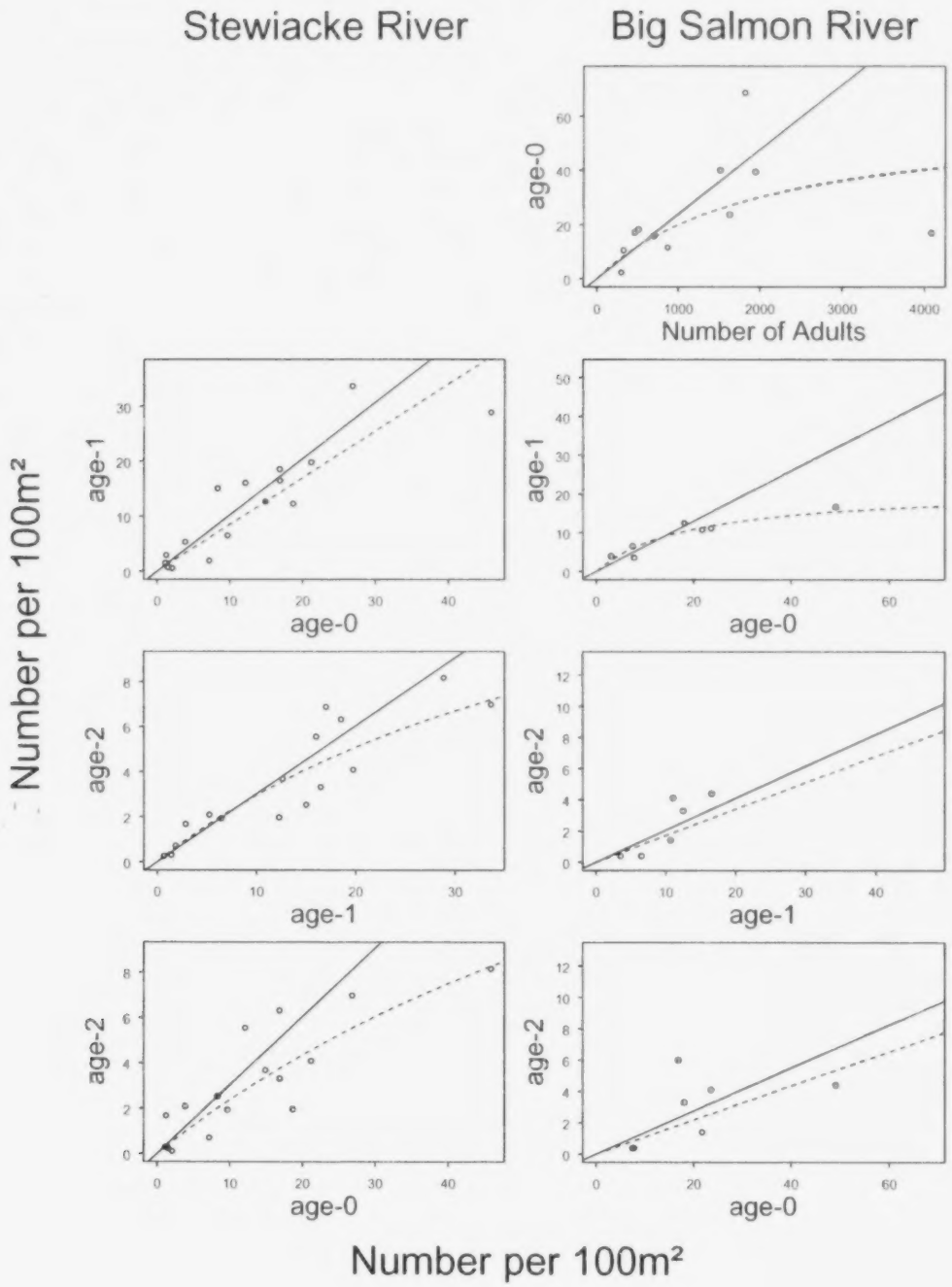

Figure 3.1. Scatterplots comparing the abundance of salmon within a cohort at different ages for early life stages of Atlantic salmon in two inner Bay of Fundy Rivers. Each dot represents the density of a single cohort at two ages. Two models were fit to each dataset: a linear (density-independent) model (solid line) and a Beverton-Holt (density-dependent) model (dashed line).

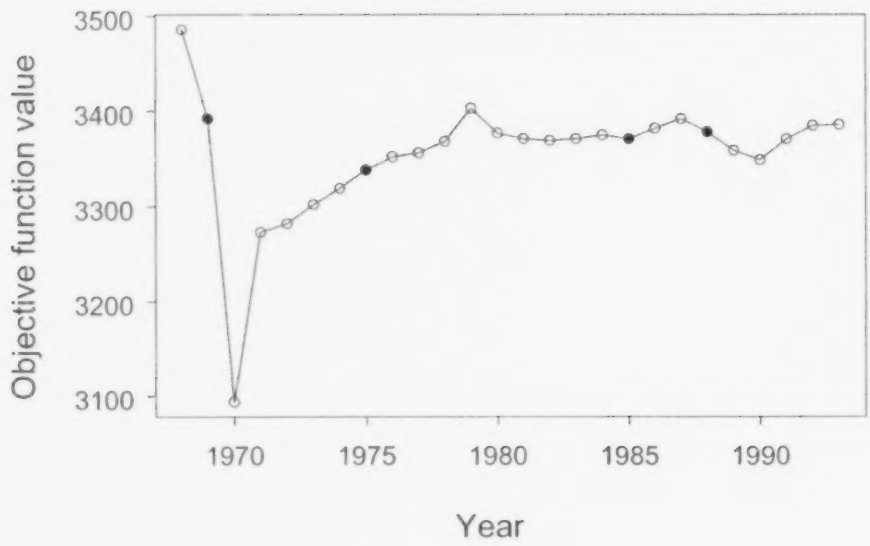

Figure 3.2. Relationship between the break year and objective function value for the marine model. The objective function values are the summed negative log likelihoods in Table 3.4. Smaller values indicate a better model fit. Break years when the hessian matrix was not positive definite are indicated with black dots.

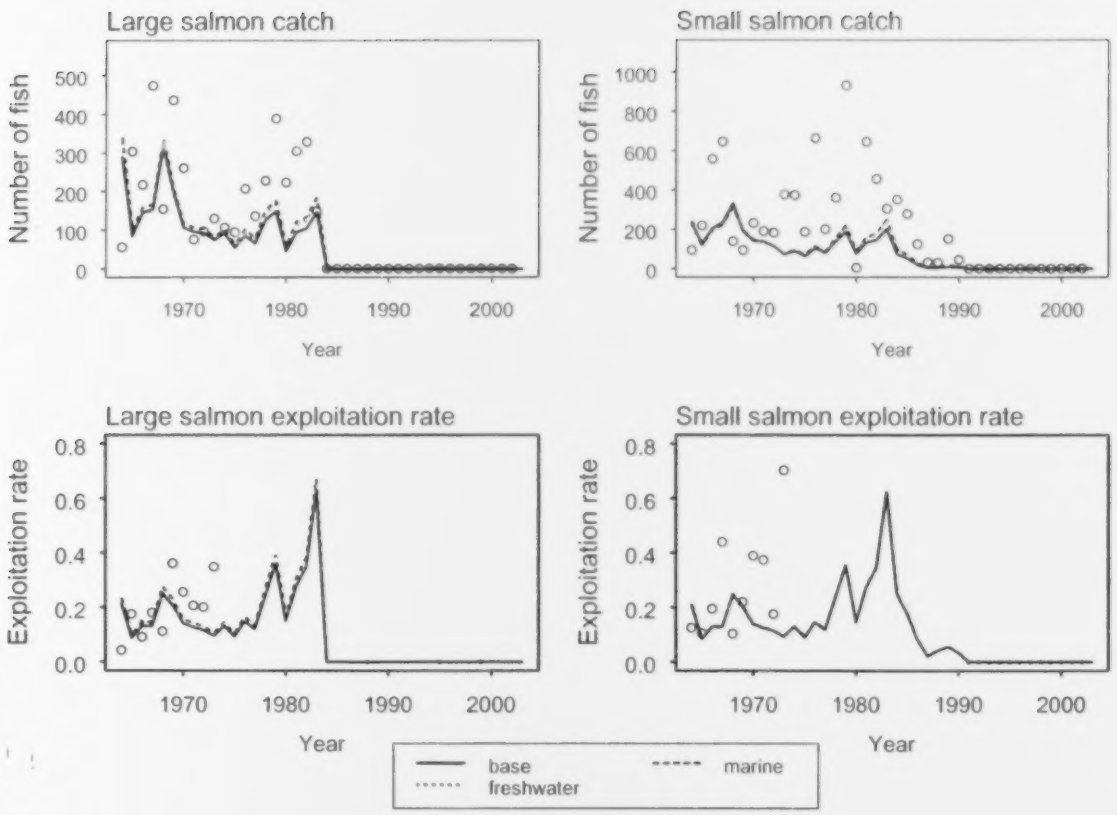

Figure 3.3. Estimated (lines) and observed (points) catches and exploitation rates for Atlantic salmon in Big Salmon River, NB, from 1964 to 2002. The three models are described in text.

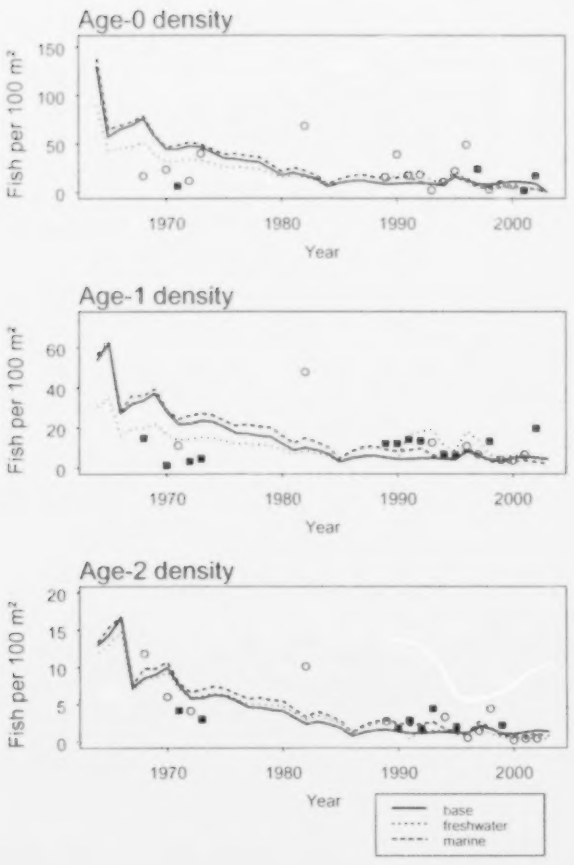

Figure 3.4. Estimated (lines) and observed (points) mean densities of age-0, age-1 and age-2 Atlantic salmon in the Big Salmon River, NB, from 1964 to 2002. The three model formulations are described in text.

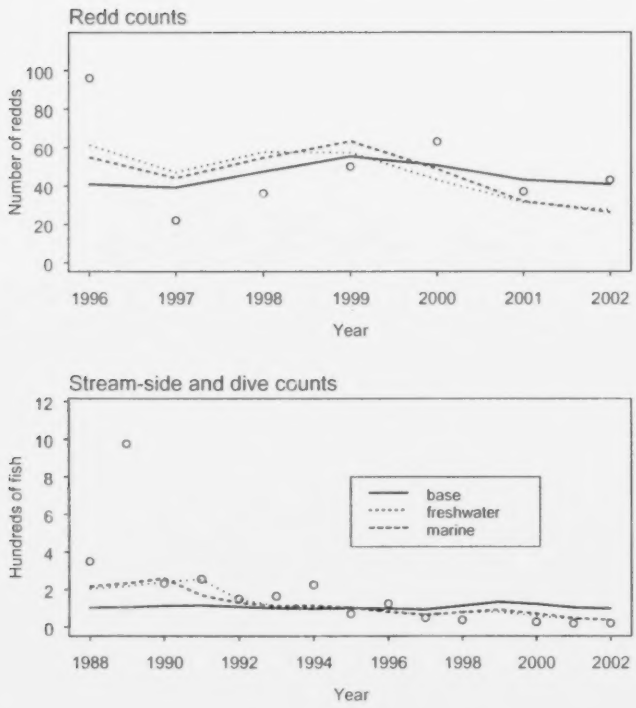

Figure 3.5. Estimated (lines) and observed (points) counts of salmon redds and number of Atlantic salmon observed by dive and streamside observation in the Big Salmon River, NB, from 1988 to 2002. The three models are described in text. Note that the time scales on the two graphs are different.

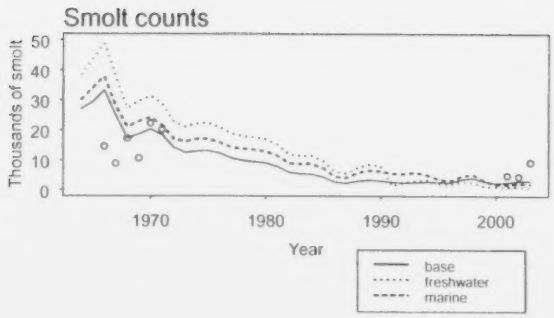

Figure 3.6. Estimated (lines) and observed (points) number of smolts emigrating from the Big Salmon River, NB, from 1964 to 2002. The three models are described in text.

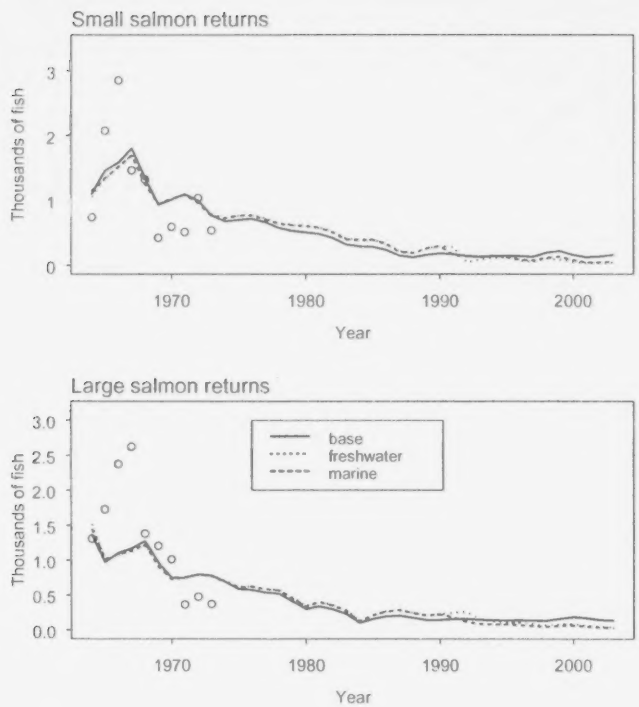

Figure 3.7. Estimated (lines) and observed (points) number of Atlantic salmon returning to the Big Salmon River, NB, from 1964 to 2002. Observations were collected by counting salmon at a counting fence operated from 1964 to 1973. The three models are described in text.

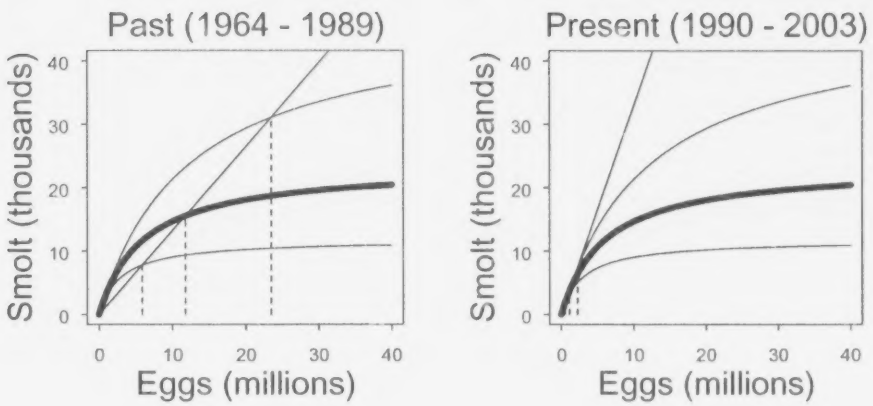

Figure 3.8. Spawner-recruit relationships (curved solid lines) for salmon of the Big Salmon River, NB. The heavy line is the fitted relationship from the statistical model. The thinner lines are the relationships that would result if the quantity of habitat was doubled (upper line) or halved (lower line). The solid straight lines are the replacement lines based on the rate at which smolts produce eggs throughout their lives. The dashed lines show the equilibrium population sizes that result given the present amount of freshwater habitat, if the amount of freshwater habitat was doubled and if the amount of freshwater habitat was halved. Equilibrium population size is much less sensitive to the amount of freshwater habitat at present marine survival rates than at past marine survival rates.

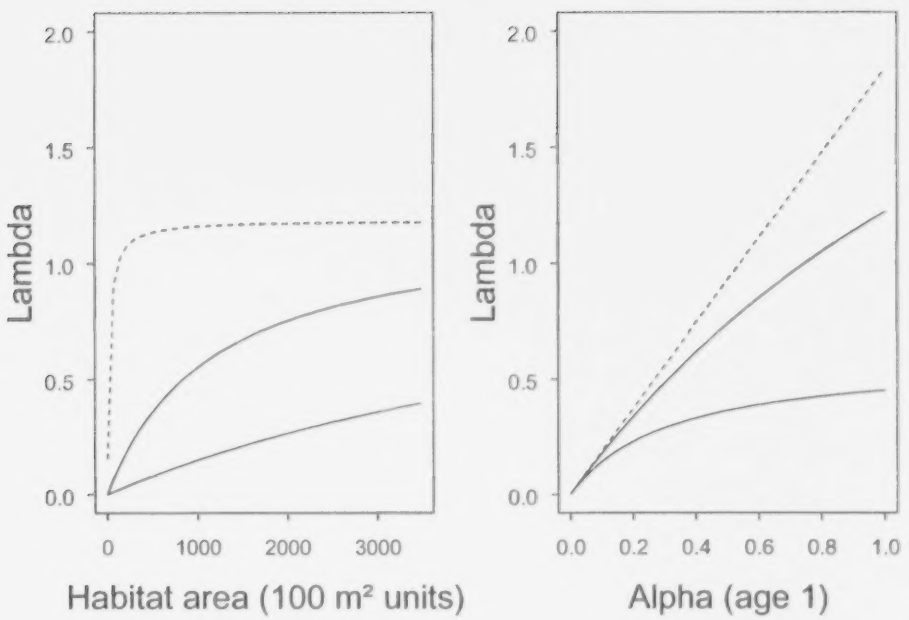

Figure 3.9. The effects of habitat area and alpha (the maximum rate at which age-0 parr produce age-1 parr) on lifetime reproductive success (lambda) for three population sizes at present (1990's) marine survival rates. Upper dashed line is at current abundance (10 salmon), upper solid line is at a conservation level (500 salmon), and lower solid line is at past abundance (3000 fish).

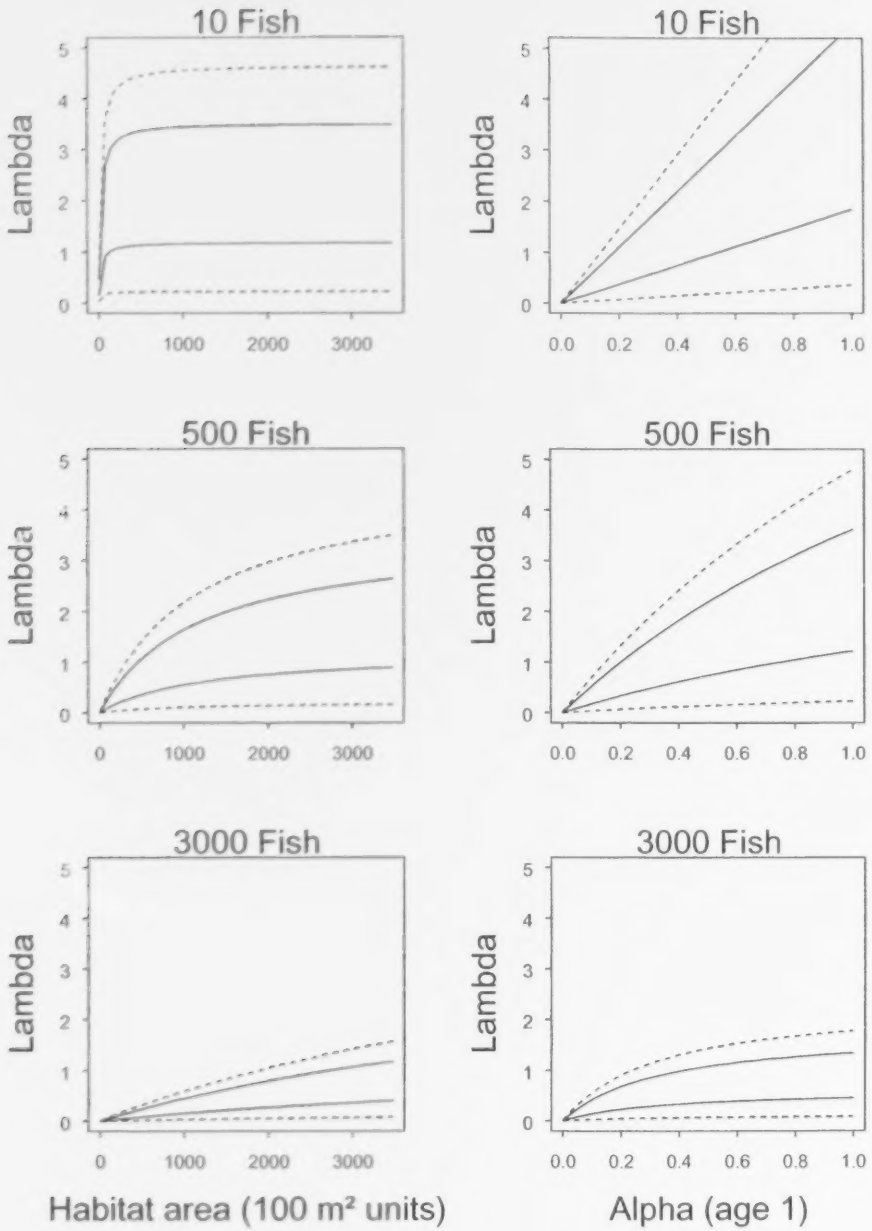

Figure 3.10. The relationships between post-smolt mortality, habitat area and density independent survival (age-0 to age-1), and lifetime reproductive success (lambda) at three population sizes (present, conservation, past) for Atlantic salmon in the Big Salmon River, NB. Each line represents a different marine mortality rate for post-smolts. Mortality rates are: upper dashed line = 0.8, upper solid line = 0.85, lower solid line = 0.95, lower dashed line = 0.99.

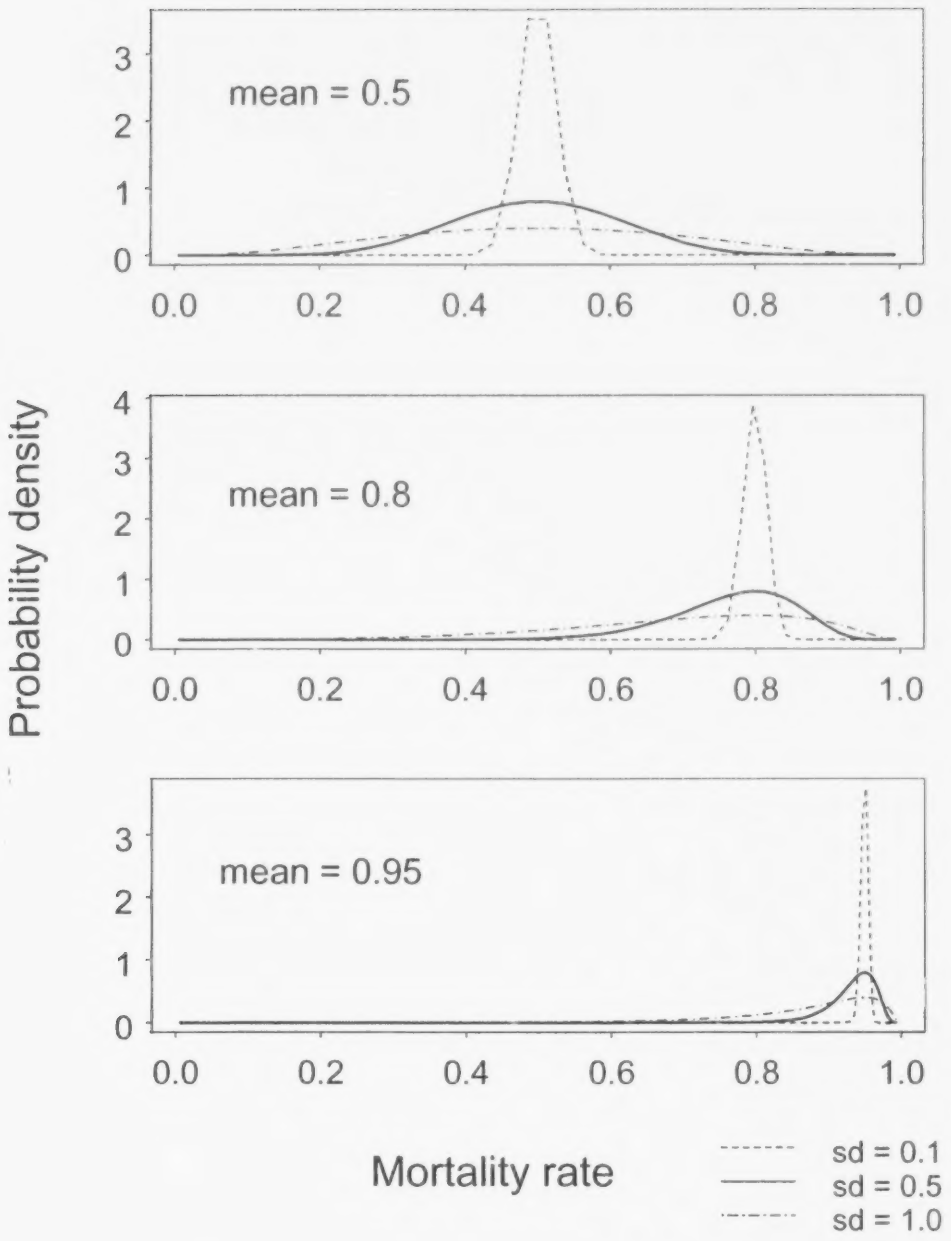

Fig. 3.11. Examples of distributions used to introduce random variability into the PVA. The standard deviation (sd) is the standard deviation of a normal distribution. The graph shows the corresponding distribution for a proportion obtained via a logit transformation.

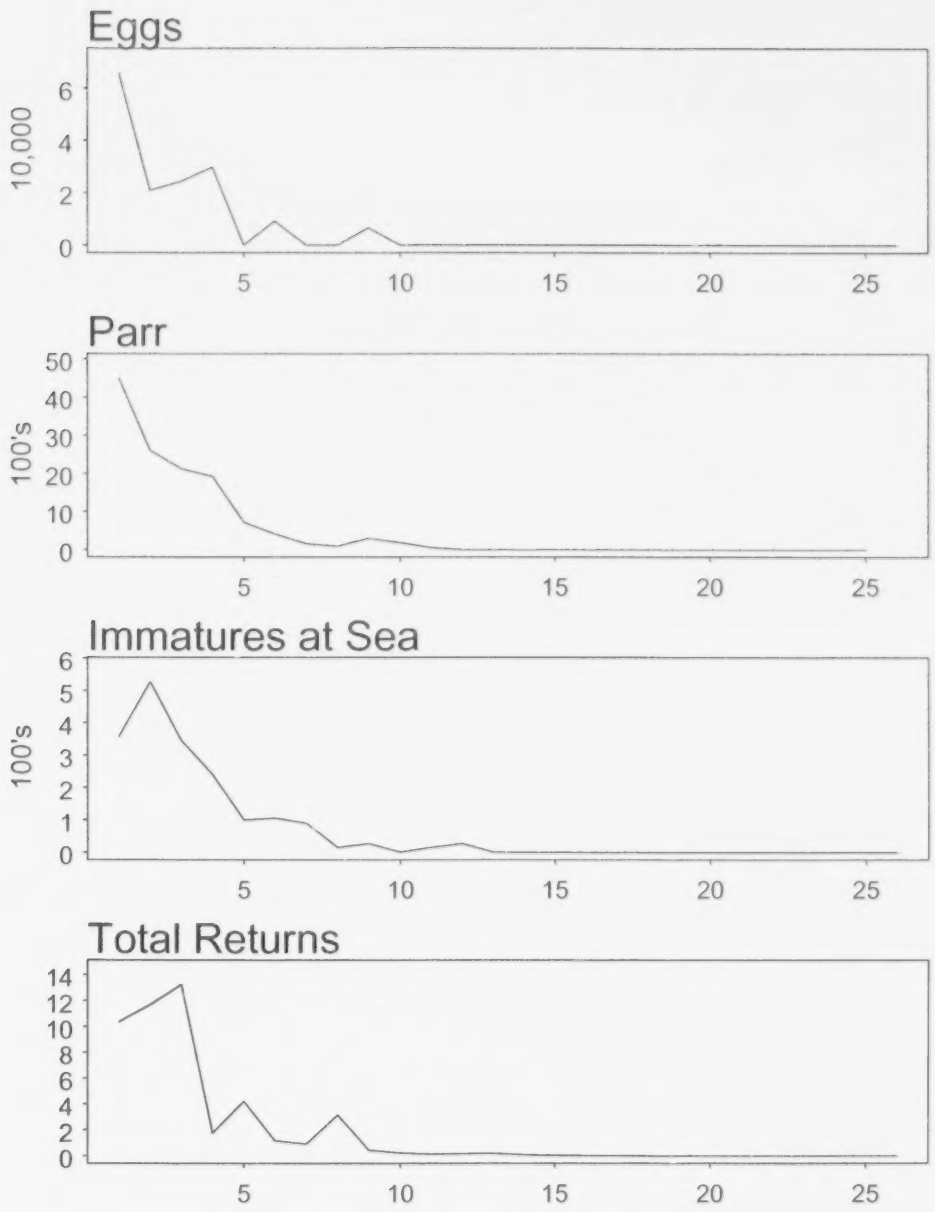

Figure 3.12. Example of a single run of the PVA model using parameter estimates obtained for the post-1990 time period using the model with changes occurring in the marine environment (Table 3.5). The population was initialized at 15 small and 15 large adult fish.

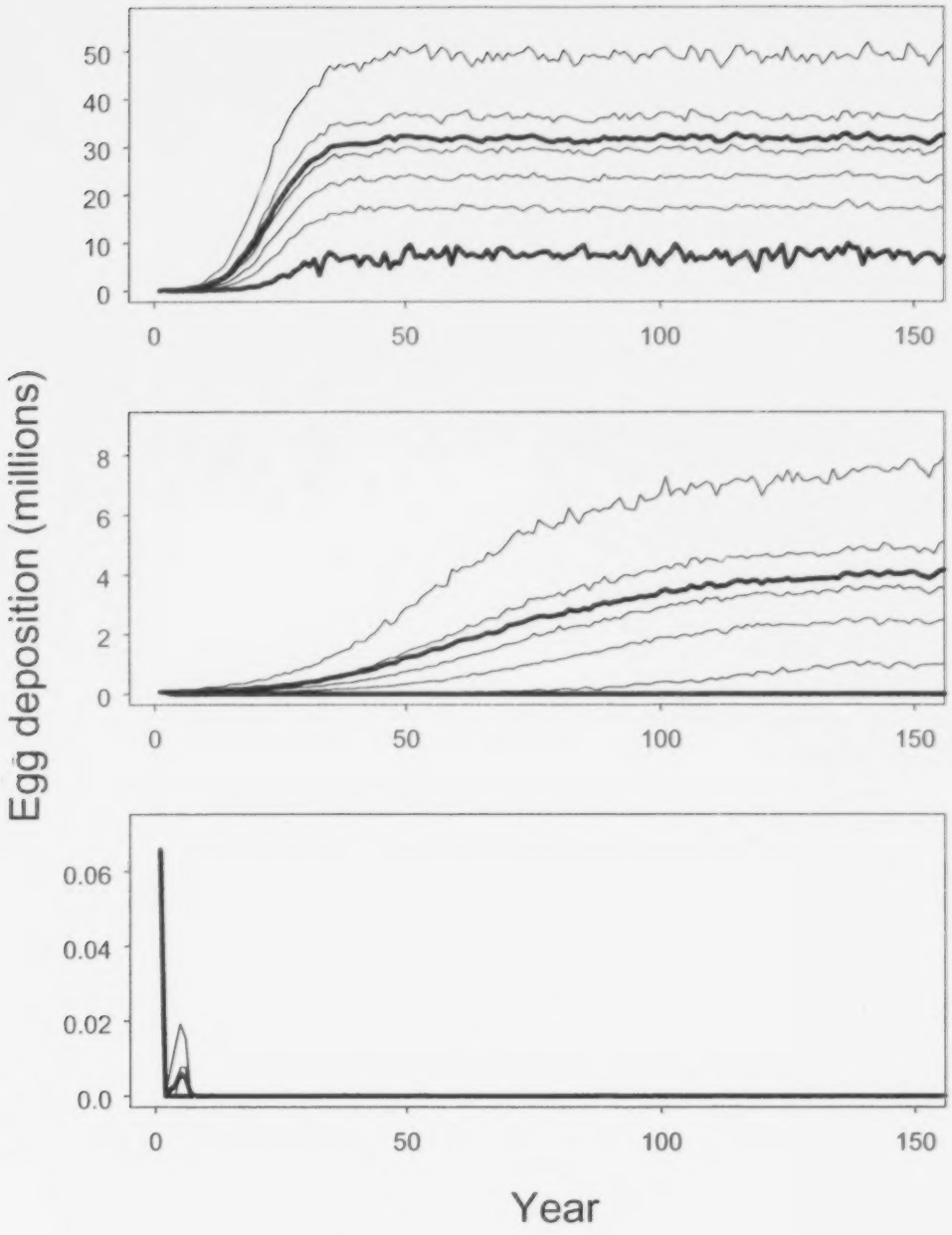

Figure 3.13. Summary of 1000 iterations of the PVA model for each of three values for annual mortality of immature salmon at sea: 0.84 (top), 0.94 (middle) and 0.99 (bottom). The light lines show the 10^{th}, 30^{th}, 50^{th}, 70^{th} and 90^{th} percentiles of egg abundance for the 1000 iterations. The darker lines show the minimum and mean abundance. This model run was initialized at 15 large and 15 small adults.

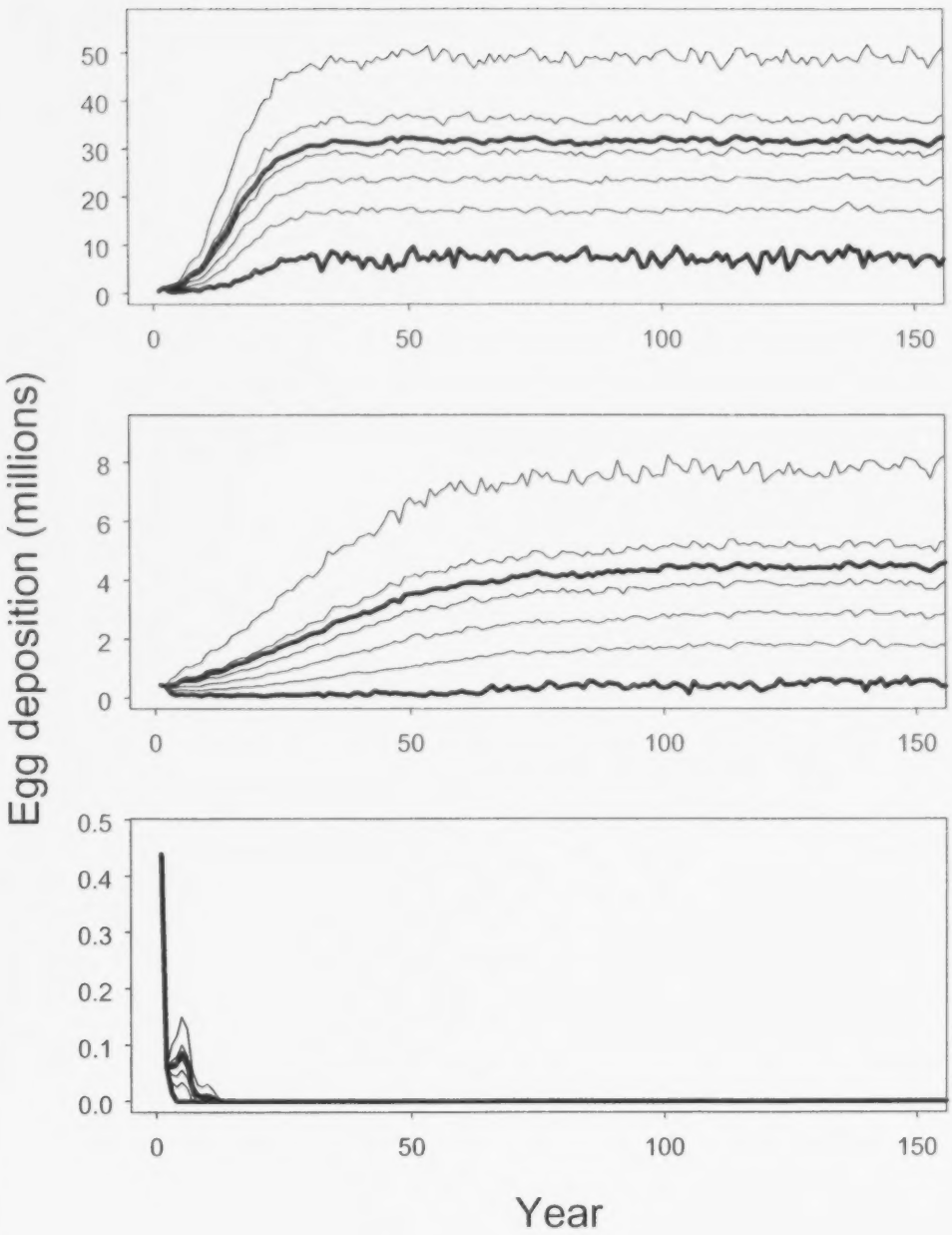

Figure 3.14. Summary of 1000 iterations of the PVA model for each of three values for annual mortality of immature salmon at sea: 0.84 (top), 0.94 (middle) and 0.99 (bottom). The light lines show the 10^{th}, 30^{th}, 50^{th}, 70^{th} and 90^{th} percentiles of egg abundance for the 1000 iterations. The darker lines show the minimum and mean abundance. This model run was initialized at 100 large and 100 small adults.

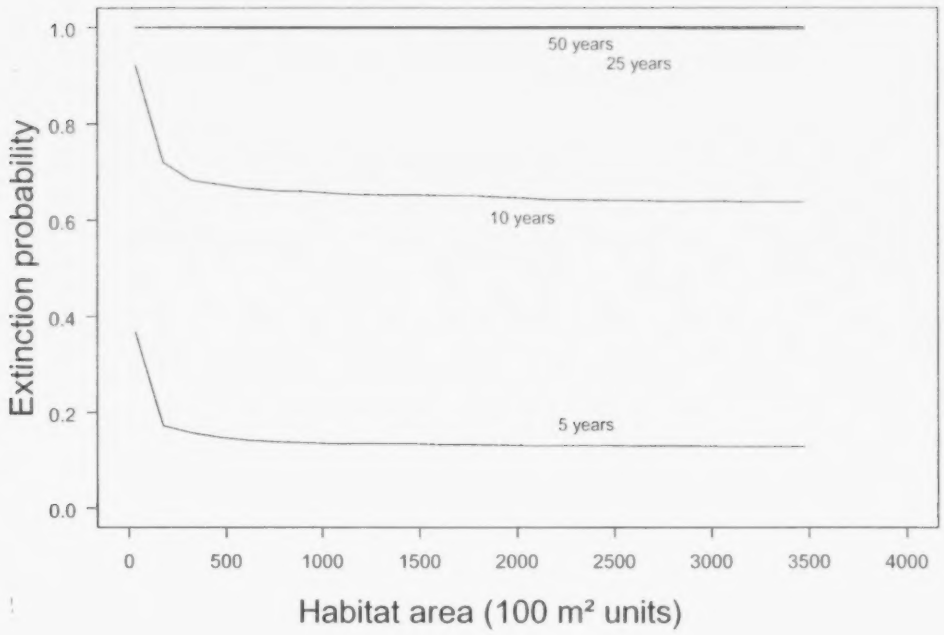

Figure 3.15. The relationship between freshwater habitat area and the probability of population extinction for Atlantic salmon in the Big Salmon River. Each line is for a separate time horizon. Extinction probabilities are calculated as the proportion of the 1000 simulated populations that are extinct for a given time period and habitat amount. The starting adult population size is 30 salmon (15 large and 15 small).

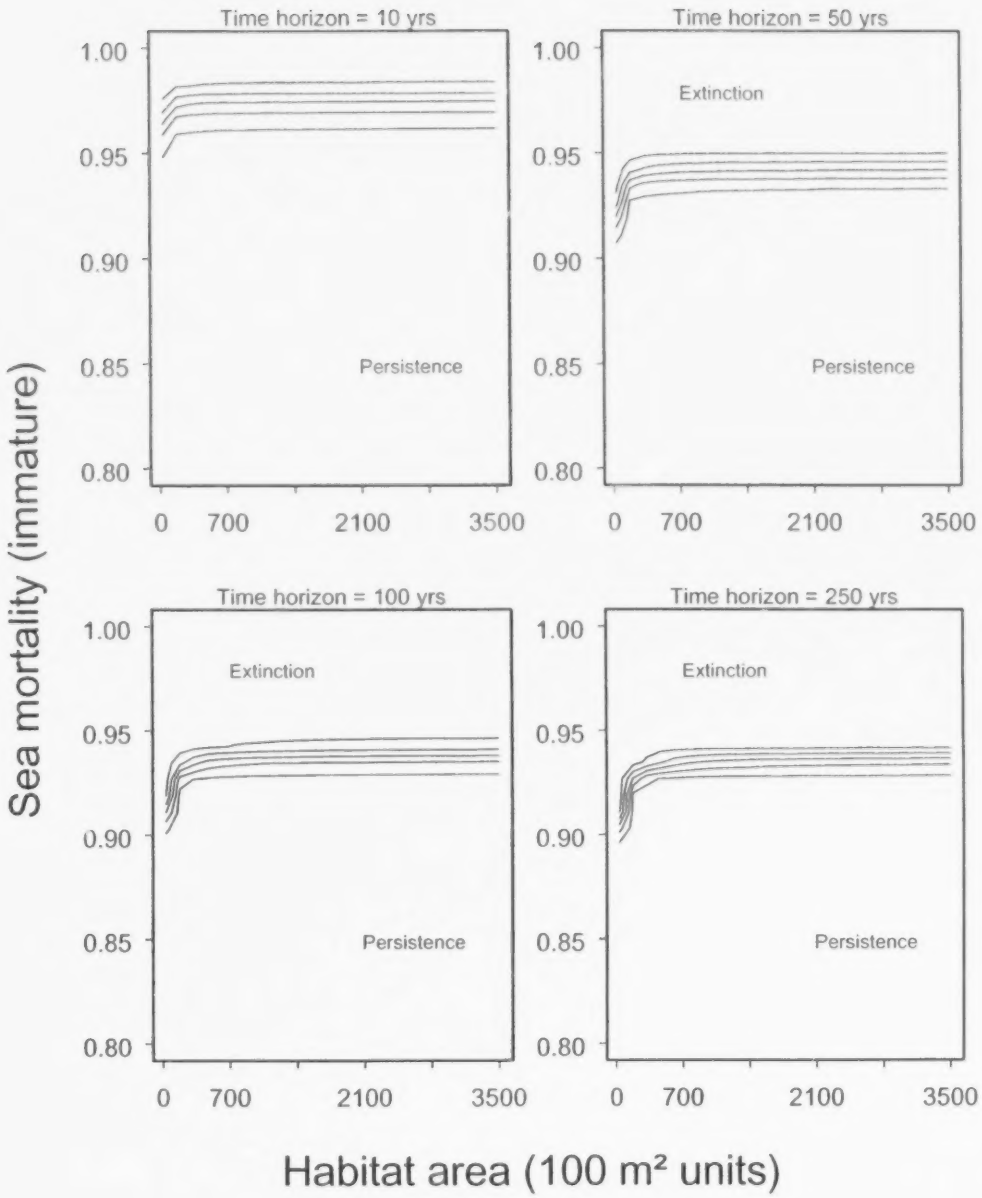

Figure 3.16. Contour plot showing how population persistence is influenced by freshwater habitat amount and annual mortality of immature salmon at sea. Each graph is for a separate time horizon. Persistence probability is calculated as the proportion of 1000 simulated populations that were not extinct within the given time horizon. Lines represent the contours of the probability of persistence from high (bottom line = 0.9) to low (top line = 0.1).

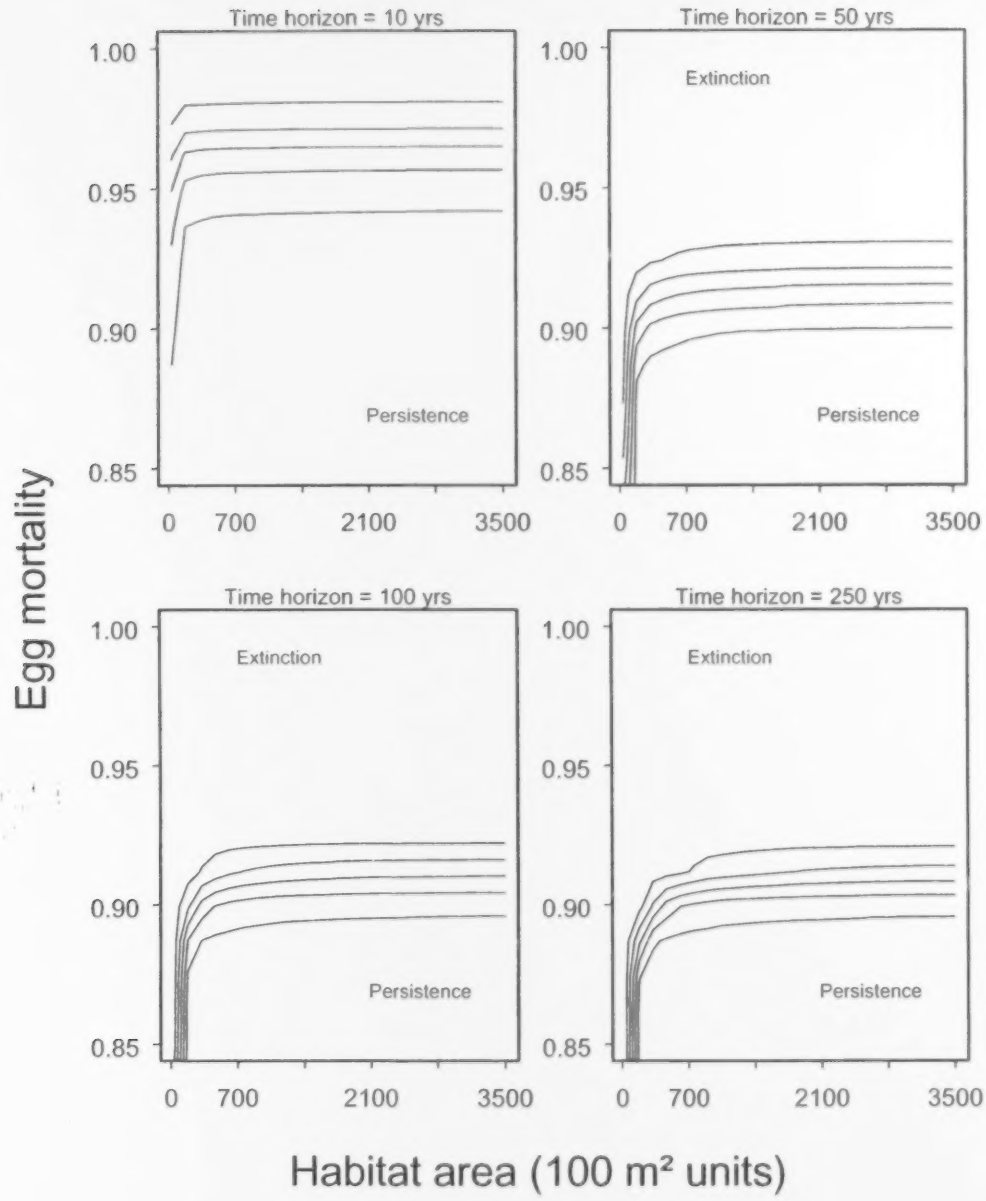

Figure 3.17. Contour plot showing how population persistence is influenced by freshwater habitat amount and egg mortality. Each graph is for a separate time horizon. Persistence probability is calculated as the proportion of 1000 simulated populations that were not extinct within the given time horizon. Lines represent the contours of the probability of persistence from high (bottom line = 0.9) to low (top line = 0.1).

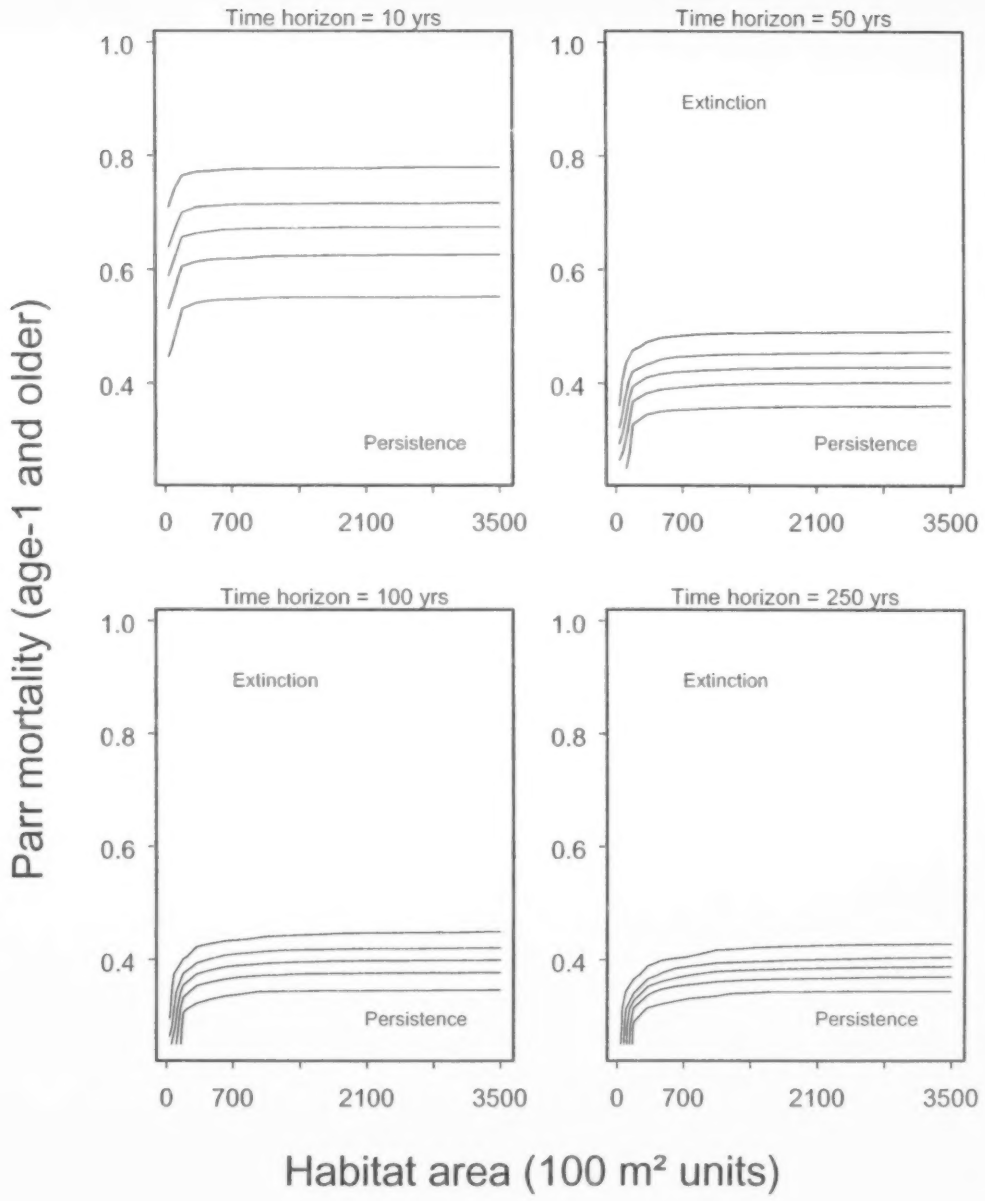

Figure 3.18. Contour plot showing how population persistence is influenced by freshwater habitat amount and annual mortality of age-1 and older parr. Each graph is for a separate time horizon. Persistence probability is calculated as the proportion of 1000 simulated populations that were not extinct within the given time horizon. Lines represent the contours of the probability of persistence from high (bottom line = 0.9) to low (top line = 0.1).

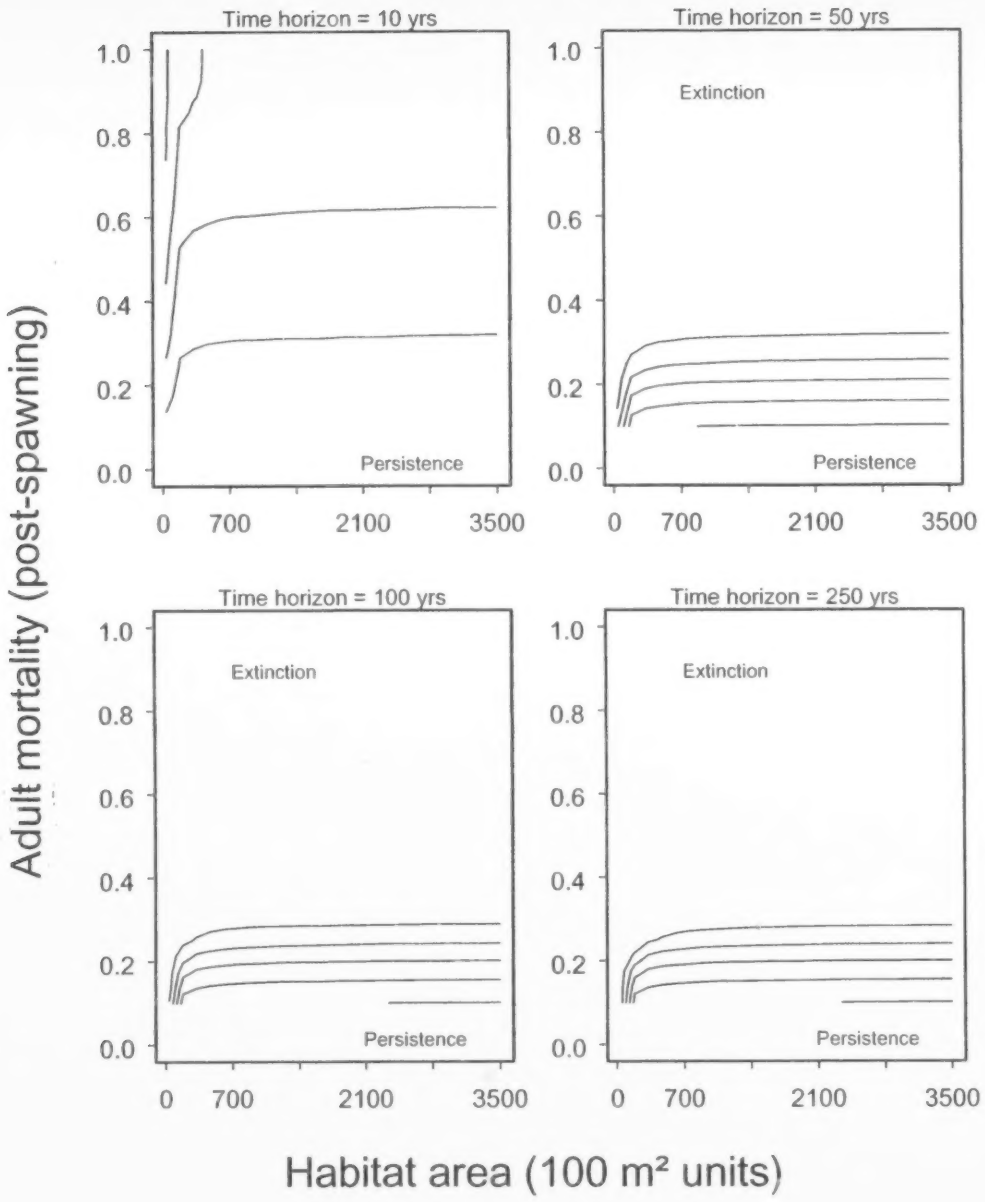

Figure 3.19. Contour plot showing how population persistence is influenced by freshwater habitat amount and annual mortality of post-spawning adults. Each graph is for a separate time horizon. Persistence probability is calculated as the proportion of 1000 simulated populations that were not extinct within the given time horizon. Lines represent the contours of the probability of persistence from high (bottom line = 0.9) to low (top line = 0.1

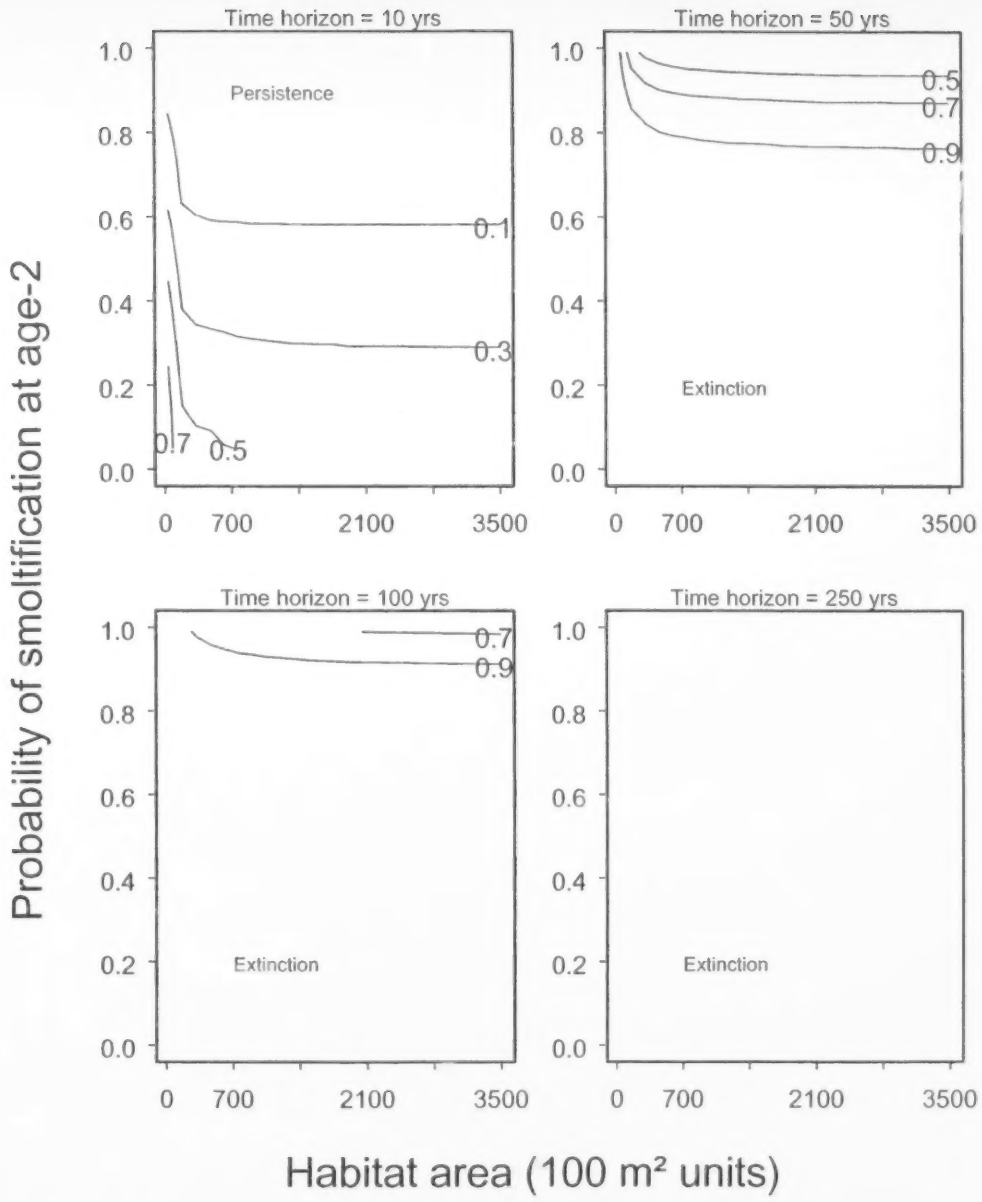

Figure 3.20. Contour plot showing how population persistence is influenced by freshwater habitat amount and the probability of smoltification at age-2. Each graph is for a separate time horizon. Persistence probability is calculated as the proportion of 1000 simulated populations that were not extinct within the given time horizon. Lines represent the contours of the probability of persistence from high (bottom line = 0.9) to low (top line = 0.1).

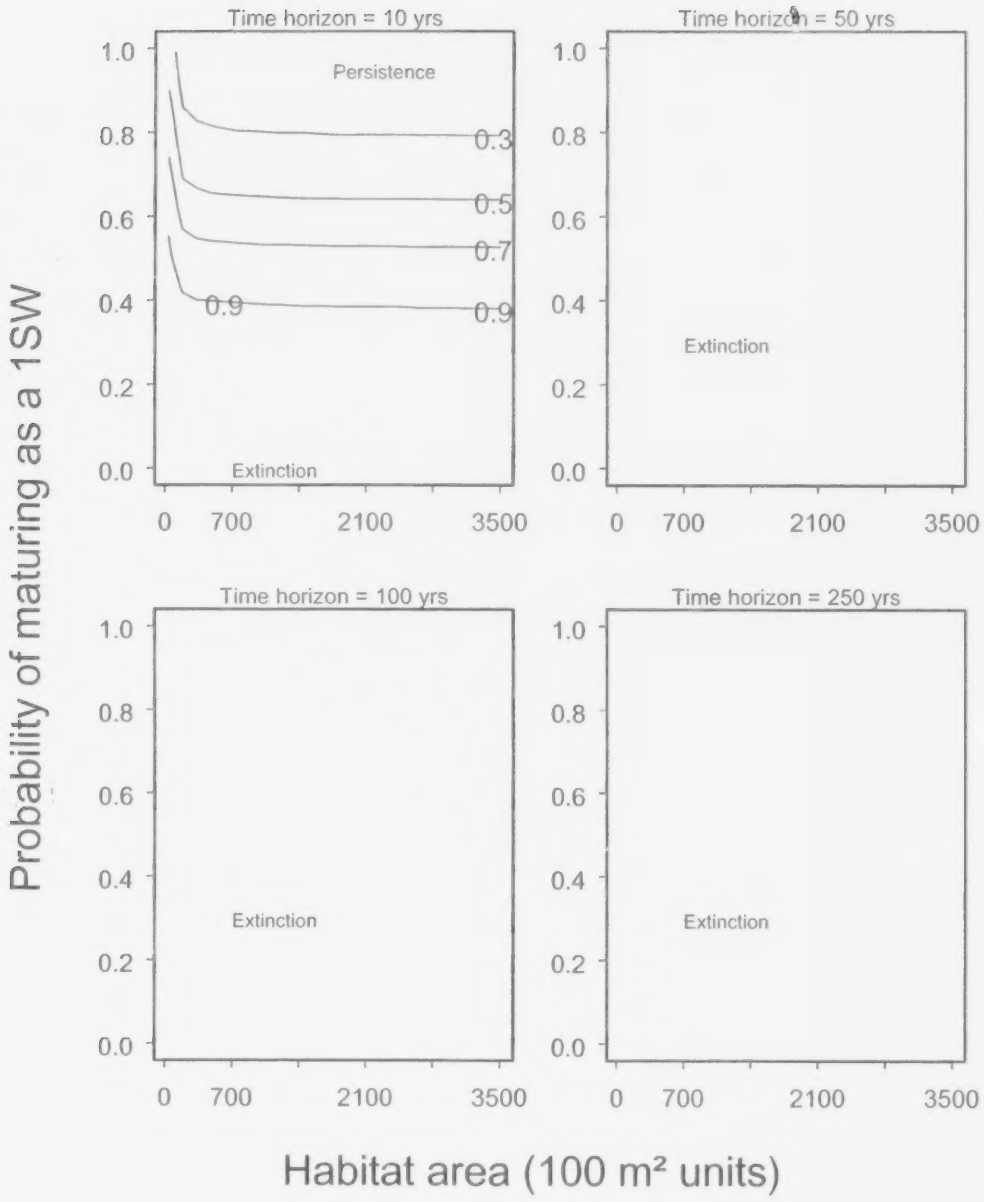

Figure 3.21. Contour plot showing how population persistence is influenced by freshwater habitat amount and the probability of maturing after one winter at sea. Each graph is for a separate time horizon. Persistence probability is calculated as the proportion of 1000 simulated populations that were not extinct within the given time horizon. Lines represent the contours of the probability of persistence from high (bottom line = 0.9) to low (top line = 0.1).

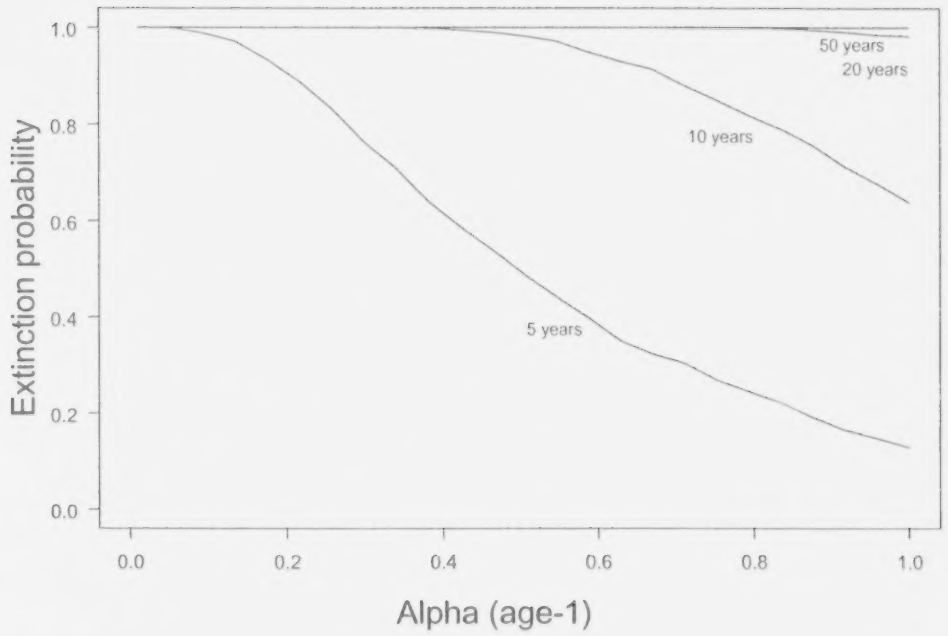

Figure 3.22. The relationship between the slope at the origin of the SR relationship used to model density dependent survival for parr between age-0 and age-1 (alpha) and the probability of extinction. Each line is for a separate time horizon. Extinction probabilities are calculated as the proportion of 1000 simulated populations that went extinct within the specified time period.